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FIELDIANA Zoology

Published by Field Museum of Natural History

Volume 70, No. 3

December 31, 1976

The Larval Characters of Featherwing and Limulodid Beetles and their Family Relationships in the Staphylinioidea (Coleoptera: Ptiliidae and Limulodidae)¹

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ABSTRACT

The family Ptiliidae, which contains the smallest known beetles, is defined and distinguished from related families in the Staphylinioidea on the basis of the larval characters of the following eight genera from the United States and Panama, which are described and illustrated: *Nossidium*, *Pteryx*, *Actidium*, *Nanosella*, *Throscopitilium*, *Actinopteryx*, *Acrotrichis*, and *Nephanes*. These genera represent several diverse elements in the family and include specialized forms like *Acrotrichis* and *Nephanes*, as well as *Nossidium*, the most generalized genus in the family.

The larval characters of the closely related Limulodidae, a family composed of obligate ant associates in the New World and the Australian region, were previously based solely upon a supposed larva of *Cephaloplectus* from Costa Rica. This larva is considered to be wrongly associated and to belong instead to the Staphylinidae (probably Aleocharinae). However a larva of *Limulodes* from Illinois is described and illustrated, making it possible to characterize the Limulodidae in a preliminary way on the basis of the larval characters of a generalized genus, and to compare the larval characters with those of the Ptiliidae and other related families.

The two families belong to the Staphylinioidea, a superfamily that contains about 10 generally recognized families, including the diverse and huge family Staphylinidae of more than 30,000 species. Within this superfamily, the two families share a presumably unique and derived feature — the fringed galea of the maxilla — with the Leptinidae, Leiodidae, and the Hydraenidae. The family Hydraenidae is often considered to belong to the superfamily Hydrophiloidea, but the larvae have a number of staphylinoid features (as noted by previous workers) and in *Hydraena* (but not in *Ochthebius* and *Meropathus*) possess a fringed galea which clearly relates them to the Ptiliidae and allied families in the Staphylinioidea. This

¹This paper is dedicated to the memory of Professor Alfred E. Emerson.

Library of Congress Catalog Card No.: 76-39773

US ISSN 0015-0754

Publication 1247

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grouping of the five families essentially corresponds to the "leptinid association" of families recognized by Böving and Craighead (1931) on the basis of other larval characters. The Ptiliidae share a unique feature, in the pair of anal hooks of the anal lobe of the tenth abdominal segment, with the Hydraenidae, but are in a derived condition with respect to many other characters in that family, such as epicranial lines, clypeal suture, ocelli, distinct tergal plates, and reduction in number of segments of the urogomphi. These reductions and losses in the Ptiliidae possibly result from evolution to a smaller size. The Ptiliidae and Limulodidae are very similar in larval characters, differing mainly by the loss in the Limulodidae of the pair of anal hooks.

A modified family key to the late-instar larvae of the "leptinid association" of the Staphylinioidea is presented.

INTRODUCTION

The main purpose of this paper is to define the family Ptiliidae on the basis of larval characters and to distinguish the larvae from those of related families in the Staphylinioidea. A second purpose is to redefine the larval characters of the Limulodidae, a family that is closely related to the Ptiliidae on the basis of adult features (Seevers and Dybas, 1943). The family is confined to the New World and the Australian region and all the species are obligate associates of ants. The larval characters of the Limulodidae were previously based on a supposed larva of *Cephaloplectus* from Costa Rica (Paulian, 1941). I consider this larva to be wrongly associated with *Cephaloplectus*, which is a highly specialized genus in the family; from the illustrations and description, the larva appears to belong to the Staphylinidae, possibly a genus of Aleocharinae. However, a larva of *Limulodes parki* Seevers and Dybas, from Illinois, is described in the present paper, and this makes it possible to characterize the family in a preliminary way, on the basis of a generalized genus, and to compare its characters with those of the Ptiliidae and other related families.

The two families belong to the Staphylinioidea, a superfamily that contains about 10 generally recognized families (see, for example, Paulian, 1941; Crowson, 1955) and more than 40,000 species. By far the largest family in the superfamily (and among the largest in the whole order Coleoptera) is the Staphylinidae, with about 30,000 described species. The Staphylinioidea constitutes a very diverse grouping of about 45 recognized subfamilies and more than 100 tribes. The relationships among these higher categories in the Staphylinioidea are very poorly understood (Crowson, 1955, 1960) and a much better knowledge of both adult and larval characters and of their distribution among the higher taxa is needed before

much progress can be made toward a phylogeny of the Staphylinoidae. This paper is intended as a contribution toward that goal.

Featherwing beetles are the smallest beetles known; in the adult stage they range in size between 0.35 and 2.0 mm., but most species fall between 0.5 and 0.9 mm. in length. Late-instar larvae are correspondingly small, mostly 1.0 - 2.0 mm. in length. There are about 62 genera and about 400 nominal species of Ptiliidae described. Judging by the extensive collections of this family in Field Museum, only a small part of the species have been named — certainly less than 10 per cent. Apart from earlier accounts that are only of historical interest (Perris, 1853, 1862; Matthews, 1872), larvae of Ptiliidae have been described by Böving and Craighead, 1931 (*Nossidium*); Hinton, 1941 (*Acrotrichis*); and Paulian, 1941 (*Acrotrichis*, *Ptinella*, *Mycophagus*, *Cylindrosella*). There are a number of inconsistencies and misinterpretations in these few accounts, as might be expected with such tiny and delicate larvae. These discrepancies will be discussed under the appropriate genera in the descriptive treatments that follow.

LIFE CYCLE AND NATURAL HISTORY

Featherwing beetle larvae are active little forms that occur together with the adults in habitats such as tree-holes, decaying logs, decaying fungi, compost heaps, animal dung, kelp on marine shores, and other moist decaying organic material. They have a characteristic jerky running behavior, like the adults. Larvae of *Nanosella* and allied genera live along with the adults in the spore tubes of Polyporaceae. When the fungus is disturbed the larvae can be seen popping in and out of the spore tubes and crossing the under surface for short distances. They are so small that they are not easy to see even with a 10× hand lens unless the under surface of the fungus is dark and contrasts with the white larvae.

Under favorable conditions featherwing beetles appear to reproduce continuously, rather than seasonally, as evidenced by finding larvae together with both teneral and fully hardened adults at different times of the year. Only one egg is matured in the abdomen at a time and this egg is relatively huge; in *Bambara*, for example, the egg is about 0.32 mm. long, or nearly one-half the length of the adult female (Dybas, 1966). The only information on the length of the developmental period (Hinton, 1941) suggests that it requires about three weeks for development from egg to adult (in *Acrotrichis fascicularis* Herbst). The number of instars is not known. The pupal

stage has been described in only one species, *Acrotrichis fascicularis* (Herbst) (Hinton, 1941).

As Hinton (1941) points out, the earlier reports that featherwing beetle larvae are predators (Perris, 1853; Matthews, 1872) are definitely wrong. The mouthparts are clearly not adapted for a carnivorous mode of life; the maxillae form little scrapers and brushes, and the mandibles have greatly enlarged denticulate molar bases for crushing and grinding food materials. The gut contents of both adults and larvae usually contain fungus spores, along with indeterminate organic matter. In the species that inhabit the spore tubes of polypore fungi, the guts of both adults and larvae are packed with spores only. This was also the case in the free-living larvae of *Nossidium* (and their associated adults) that are described in this paper. It is highly probable therefore that the main feeding adaptation of Ptiliidae is for feeding upon spores and hyphae of fungi and, probably, soft decaying organic materials containing micro-organisms.

MATERIALS AND METHODS

The larvae in this study were mounted from 70 per cent ethanol in which they were stored, directly into Hoyer's medium on microscope slides, or were first treated with cold KOH and then mounted in glycerine gel. In some instances they were lightly stained with Mercurochrome.

Larvae were normally studied at magnifications up to 500 \times , mostly with phase-contrast optics. Some structures (e.g., the fimbriate galea) were examined under oil immersion at 1,250 \times . The illustrations were made using a Wild M-20 compound microscope with drawing tube attachment. All the illustrations were prepared and inked by me.

The larval assignments to genus in this study were based upon field associations with the adults; none were reared. In the family Ptiliidae, this procedure is probably not a significant source of error because, as stated earlier, featherwing beetles reproduce continually under favorable conditions and both adults and larvae live in the same habitat and can be found together at the same time, often in large numbers. For each of the genera described in this paper, there are replicate field associations as well. The one exception is *Limulodes* whose association is based on one collection consisting of only three larvae. The reasons for regarding these specimens as the previously undescribed larvae of *Limulodes* are given in the treatment of that genus later in the paper.

Most of the larvae described in this paper are identified only to genus. The species of the associated adults can be readily discriminated (especially by their distinctive spermathecae) but the genera need to be revised before species names can be correctly applied, even to some of our most common species. Identification of the larvae only to the genus level is not, however, a serious limitation in the context of a study like this which is concerned mainly with family characters and relationships.

ABBREVIATIONS USED IN ILLUSTRATIONS

a	antenna
a1	antenna, segment 1
a2	antenna, segment 2
a3	antenna, segment 3
abI etc.	abdomen, segment I etc.
ah	anal hook
ant	anterior
ap	apical processes or styles
asa	accessory sensory appendage
av	anal vesicle
c	coxa
ca	cardo
cl	tarsungulus (claw)
co	condyle (ventral) of mandible
d	denticles
df	dorsal fringe of galea
di	digitiform organ
es	pigmented eyespot
fe	femur
fga	fimbriate "galea"
la	lacinia
lb	labrum
li	ligula
lp	labial palpus
lt	labral teeth
ma	mandible
me	mentum

mes	mesothorax
met	metathorax
mo	molar area
mp	maxillary palpus
mp1	maxillary palpus segment 1
mp2	maxillary palpus segment 2
mp3	maxillary palpus segment 3

p	pore
pf	palpifer
pm	prementum
pr	prostheca
pro	prothorax

s	sternum
sa	sensory appendage
sm	submentum
so	sensory organ
sp	spiracle
st	maxillary stipes

te	tentorium
ti	tibia
tr	trochanter
tt	terminal tuft (mp3)

ur	urogomphus
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vf	ventral fringe of galea
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SYSTEMATICS

PTILIIDAE - FAMILY CHARACTERS BASED ON LARVAE

Family Diagnosis. — The larvae of Ptiliidae can be distinguished from other Staphylinioidea by the following combination of characters: size small, mostly less than 2.0 mm.; body form linear; head directed downward; head and thorax very little wider than the abdominal segments just behind, subcylindrical; color white or very slightly yellowish, very lightly sclerotized; tergal and sternal sclerites not or very faintly defined; setae simple; ocelli or eyespots absent (except in *Nossidium* (s.l.) from Panama which has a single pigmented eyespot on each side of the head capsule); epicranial and frontal lines lacking (faintly indicated by thinner portions of the

cuticle in one specimen of *Acrotrichis* from Oregon); abdomen 10-segmented and possessing a membranous anal vesicle which is furnished with a pair of retractile claws or anal hooks; urogomphi articulated, one-segmented (lacking in *Nanosella* and related fungus spore-tube inhabitants). The maxilla in some Ptiliidae (e.g., *Nossidium*) with mala more or less divided into an inner denticulate lacinia and an outer, more dorsal, fimbriate "galea" (lacking in *Nanosella* and related forms that live in the spore tubes of polypore fungi). In other Ptiliidae (e.g., *Acrotrichis*) the lacinia and fimbriate galea are apparently combined into a single structure. Mandibles symmetrical or nearly so, with a greatly expanded molar portion which is denticulate on its inner side and provided with about 6-7 rows usually, of tiny rasplike denticles usually on both ventral and dorsal surfaces; the apical part slender, and toothed or serrate before its apex; at middle on inner side with a slender articulated appendage (prostheca).

The larvae are active forms that are found, together with the adults, in decaying moist organic materials such as the forest floor, tree-holes, decaying logs, decaying fungi, animal dungs, kelp on marine shores, etc. Larvae of *Nanosella* and its allies live together with the adults in the spore tubes in fungi of the family Polyporaceae, where they feed upon the growing spores.

Family description of larvae. — Late-instar larvae mostly between 1.0 and 2.0 mm. long. Body slender, linear, and subparallel; subcylindrical in cross-section. Cuticle mostly white, or occasionally with a slightly yellowish tone. All body setae simple (slender and pointed at apex).

Head exserted, directed downward, without ocelli or eyespots (except in *Nossidium* (s.l.) from Panama in which there is a single pigmented eyespot (*es*) on each side). Epicranial lines lacking (they may be indicated in some specimens of *Acrotrichis* by faintly thinner portions of the cuticle, in the form of a short median stem and two frontal arms enclosing a V-shaped frontal region). Labrum (*lb*) transverse, free, separated by a fine suture (sometimes difficult to detect). Mandibles (*ma*) symmetrical, or very nearly so, with a greatly expanded molar area (*mo*) whose inner margin is furnished with denticles or teeth and whose dorsal and ventral surfaces (in all cases?) bear six or seven rows (usually) of minute rasp-like denticles. Apex of mandible slender, with several subapical teeth or serrations; on its inner side, near middle, is a slender, articulated process, "prostheca" (*pr* = retinaculum or lacinia mandibularis of authors). Outer margin near base with two setae.

Antennae (*a*) 3-segmented, segment two bearing 3-4 setae and a large sensory appendage (*sa*) on its inner side of varying shape (bifid in *Actidium*); this is the "hyaline vesicle," "accessory spine," or "membranous lobe" of authors. Another similar but much smaller structure termed an accessory sensory appendage (*asa*) is present in *Nossidium*. Segment 3 with about 3-4 setae and at apex with about 2-4 attenuated cuticular processes or styles, which may be long and setiform but which do not have sockets.

Maxilla with a 3-segmented palpus and an anteriorly produced maxillary lobe which is more or less divided into an inner lacinia (*la*) and an outer characteristically fimbriate "galea" (*fga*). The lacinia is furnished apically with a series of curved teeth or hooks and one or two thin knife-like laminae, and it bears a stout, blunt, subapical spine on its inner border. The galea is a more membranous lobe extending beyond the lacinia from its dorsal surface and bearing two apical fringes of hair-like processes - a larger more dorsal fringe (*df*) and a smaller ventral fringe (*vf*) (in *Acrotrichis* there is possibly a third very small, ventral fringe). The laciniae and galeal portions of the maxillary lobe are distinctly separated in *Nossidium*, a generalized genus of Ptiliidae; they are united into one structure in more derived forms (e.g., *Acrotrichis*). In *Nanosella* and related genera that live in the spore tubes of polypore fungi, the galea is reduced or lacking though this is difficult to make out because of the small size of the mouthparts. The first segment of the maxillary palpus is broad and bears two pores but no setae; the second bears two subapical setae, one inner and one outer; the third is more slender and bears on its dorsal side a basal hyaline vesicle, the "digitiform organ" (*di*) (Deleurance-Glaçon, 1963); segment three is furnished with a terminal tuft (*tt*) (sensory structures?) which was interpreted as a fourth palpal segment by Paulian (1941). A sclerite, possibly representing the palpifer (*pf*), is sometimes partly indicated at the base of the palpus on the side of the maxilla.

The prementum (*pm*) of the labium bears a pair of two-segmented subcylindrical labial palpi (*lp*), and a median lobe-like ligula (*li*) of variable form. The second segment of the palpus is terminated by pegs (sensory?) or tufts. The prementum bears one pair of setae and its posterior border is usually demarcated by a detectable line or suture, but the remaining divisions of the labium - the mentum (*me*) and submentum (*sm*) are usually not distinct or are only vaguely demarcated; the posterior region bears three pairs of setae in a median longitudinal series behind the pair on the prementum. In related Leiodidae: Catopinae: Bathysciini such as first instar larvae of *Speonomus d. delarouzei* (Deleurance-Glaçon, 1963. Pl. IV, fig. 6), the mentum and gulamentum (= submentum) bear respectively 4 and 2 erect setae in the same setal arrangement as in Ptiliidae larvae. The corresponding setae in the Ptiliidae in all probability are homologous to those in the Bathysciini and thus can be used as landmarks to define the areas of mentum and submentum when the suture between these sclerites is indistinct (or when pseudo-sutures or folds accidentally appear in the slide preparations).

The segments of the thorax are little wider than the abdomen; the tergal sclerites usually do not have distinct margins. The mesothoracic spiracle is almost always present (not detected in *Throscoptilium*); it is circular and lies behind the posterior border of the prothorax. Abdomen 10-segmented, the individual terga not or only faintly indicated; sterna never with defined sclerotized areas; spiracles (*sp*) circular, present on segments I-VIII, or (in many cases) absent or not detectable; when present they are much smaller than the mesothoracic spiracle. Segment IX with a pair of 1-segmented, articulated urogomphi (*ur*) which bear about six or seven setae and a pore on the outer side; the urogomphi are absent in *Nanosella* and other genera that live in the spore tubes of polypore fungi. Segment X cylindrical, with a membranous anal vesicle (*av*) that bears two retractile claws or anal hooks (*ah*). A long slender muscle which appears to originate from the antero-ventral part of segment VIII inserts upon the base of each claw.

Legs with 4 segments and a single claw or tarsungulus (*cl*) which has a pair of setae near middle; tibia with a pair of spines at apex.

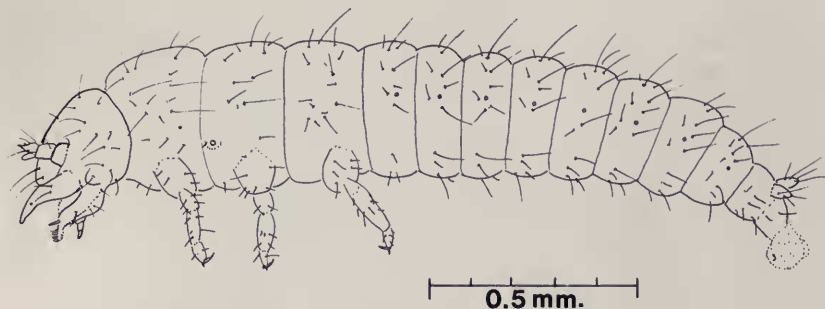


FIG. 1. *Nossidium americanum* Mots., late instar larva, lateral aspect, setal pattern approximate (see figs. 2-5 for labelled structures).

DESCRIPTIONS OF GENERA OF PTILIIDAE LARVAE

Nossidium americanum Mots. Figures 1-5.

Late-instar larva (fig. 1). Length 1.84 mm.; width across metathorax 0.34 mm. Body subparallel, subcylindrical in cross-section. Color white, becoming yellowish on head capsule, especially on labrum and mandibles; setae simple, slender, and pointed at apex; no composite setae present.

Head capsule (figs. 2a, b) lightly sclerotized, without distinct epicranial and frontal lines; clypeus not delimited by a suture; labrum more heavily sclerotized, separated by a fine suture that is difficult to see in some preparations. Ocelli absent. Antennae (fig. 3a) 3-segmented, the 2nd bearing a large sensory appendage as large as segment 3 and with a smaller accessory sensory appendage or hyaline vesicle; segment 3 small, terminating in 1 prominent and 2(?) lesser spicules; antennal setae of segments 2 and 3 as in Figure 3a. Labrum transverse (fig. 2a), about twice as broad as long, anterior margin arcuately emarginate, with a bilobed projection at middle, and with 14 setae.

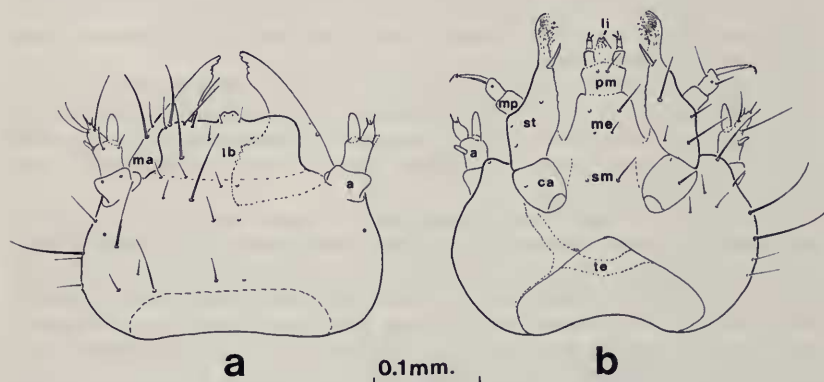


FIG. 2. *Nossidium americanum* Mots., larva, head capsule; a, dorsal aspect, maxillae not shown; b, ventral aspect, mandibles and labrum not shown.

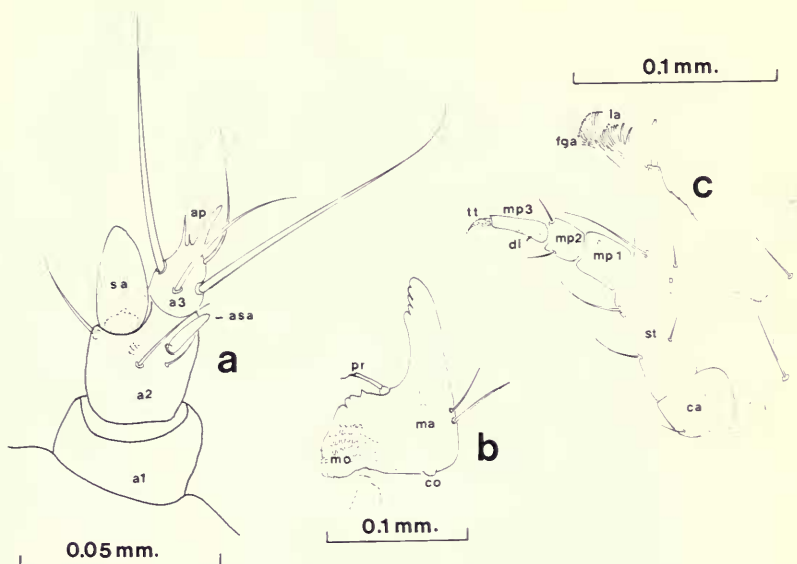


FIG. 3. *Nossidium americanum* Mots., larva: a, left antenna, ventral aspect; b, left mandible, ventral aspect; c, right maxilla (and adjacent portion of mentum), ventral aspect.

Maxilla as in Figures 2b and 3c, with 3-segmented palpus, though an additional basal division (palpifer?) is partly indicated dorsally in some preparations; the 2nd segment with 2 setae, the 3rd with a terminal tuft and with a thin-walled basal process (digitiform organ) on the dorsal side, about half as long as the segment; galea finely and regularly fringed; lacinia with a number of curved teeth, and with a stout, mesal, subapical spine. Labium with 2-segmented palpi, the second segment shorter than the first, and bearing an apical process; ligula produced, with anterior margin very slightly emarginate. Ventral sides of head capsule with form and setae as in Figure 2b; gula not defined.

Mandibles (fig. 3b) both similar, apex slender, with four subapical teeth or serrations; molar region very prominent, with about 5 rows of fine rasplike denticles on dorsal surface, and several prominent denticles on antero-mesal angle; a slender sclerotized, articulated process (prostheca) present on the inner surface; outer basal margin with 2 prominent setae.

Thorax very little broader than first abdominal segment, the terga of both thorax and abdomen not clearly defined. Dorsal setae of metanotum as in Figure 5b. Setal patterns of abdominal segments as shown in Figure 5b (dorsal), 5c (sternal), and 5d (lateral aspect). Spiracles annular, present on sides of abdominal segments I-VIII, (figs. 1, 5d). Meso-thoracic spiracle larger and located as in Figure 1. Urogomphi 1-segmented, shape and setae as in Figures 1, 4a, b. Anal vesicle of segment X with 2 sclerotized anal hooks (figs. 1, 4a).

Legs all similar in form and setae to middle leg (fig. 5a); tibia with a pair of very short, stout, apical spines; tarsungulus with a pair of very short, fine setae at middle.

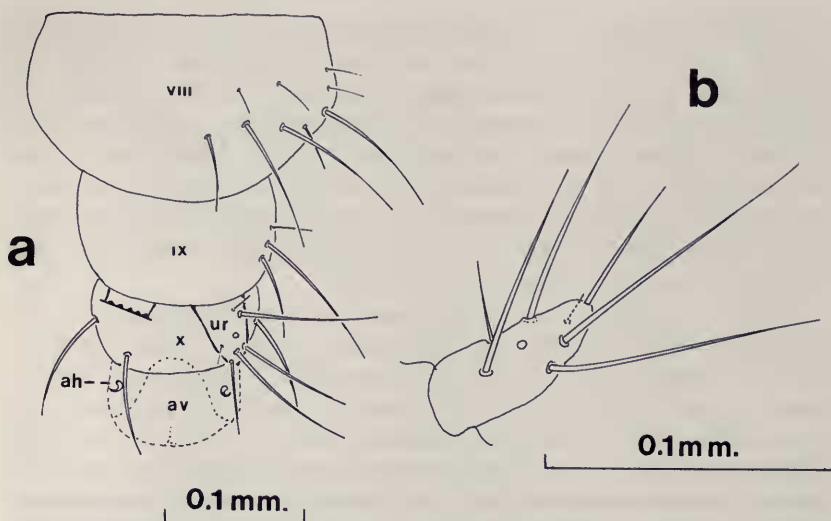


FIG. 4. *Nossidium americanum* Mots., larva: a, abdominal segments VIII-X, dorsal aspect, showing urogomphi (left urogomphus removed to show setal pattern of segment X) and membranous anal vesicle containing the two "anal hooks"; b, left urogomphus, lateral aspect.

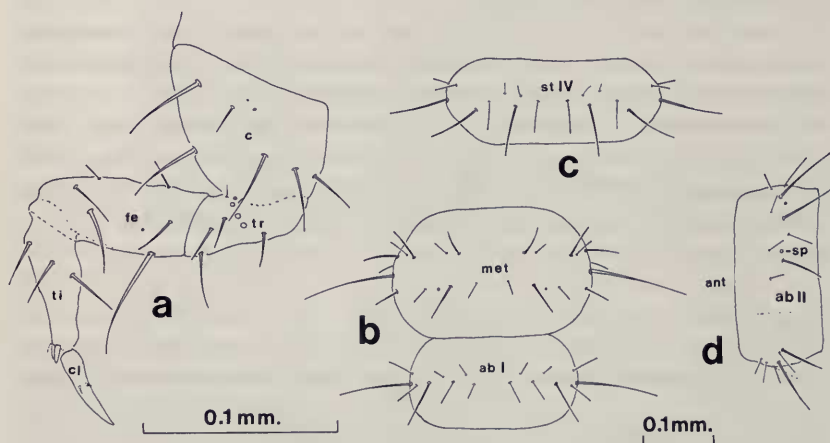


FIG. 5. *Nossidium americanum* Mots., larva: a, third right leg, anterior face; b, dorsum of metathorax and first abdominal segment, showing pattern of setae; c, ventral aspect of abdominal segment IV; d, abdominal segment II, left lateral aspect, showing spiracle and setal pattern (anterior is to left).

Material examined. — 16 larvae associated with about 2,000 adult *Nossidium americanum* Mots. collected September 2, 1962 at Funk's Grove, near Bloomington, McLean County, Illinois by Walter R. Suter. The description and illustrations were made from several different larvae. The specimens were in floor litter at the buttress of a large maple tree and were extracted by means of a Berlese funnel. This extraordinary density of adults probably represents a concentration into a moist pocket at the base of the large tree as a result of a prolonged dry period.

Remarks. — The larva of *Nossidium americanum* Mots. was previously figured by Böving and Craighead (1931). In their Plate 10, fig. L., the illustration is of the labrum not "Epipharynx"; fig. I shows a gula (labeled *gu*), but I have not been able to detect this as a defined area in my preparations (there is no gula in adult Ptiliidae); and fig. J shows a 4-segmented palpus whereas the palpus is 3-segmented in Ptiliidae larvae (possibly a partially indicated palpifer is being interpreted by these authors as a segment of the palpus). In addition to these differences in detail, the main discrepancies have to do with the two terminal "anal hooks," which, contrary to those authors, are present in *Nossidium* just as they are in the other genera described in this paper and as previously reported in *Acrotrichis* (Hinton, 1941), and in the Hydraenidae (Böving and Craighead, 1931).

The digestive tracts of the larvae, as well as of the associated adults, were solidly packed with fungus spores of uniform size, indicating that both were feeding on the same foods.

Based on adult structure, *Nossidium* and the related *Motschulskium* (from the sea shore of western North America) represent the most generalized Ptiliidae. Together with some undescribed genera, I consider them to form a distinctive group of subfamily rank in the Ptiliidae (Dybas, in prep.).

***Nossidium* (s.l.) species indet. Figure 6.**

Late-instar larva, length 1.5 mm.; width across prothorax 0.23 mm. Body similar in general to *Nossidium americanum* but more slender. Head capsule similar in form and setal pattern to *N. americanum* but with a conspicuous eyespot on each side (fig. 6a); labrum (fig. 6a) with median projection faintly 3-lobed and not 2-lobed as in *americanum*; dorsum with 3 pairs of "pores" arranged as in Figure 6a. Antennae (fig. 6b) similar to *americanum* but more slender and elongate.

Material examined. — Several larvae associated with eight imagos (part of a larger series at the Museum of Comparative Zoology, Harvard University). Collected July 31, 1969 in Barro Colorado

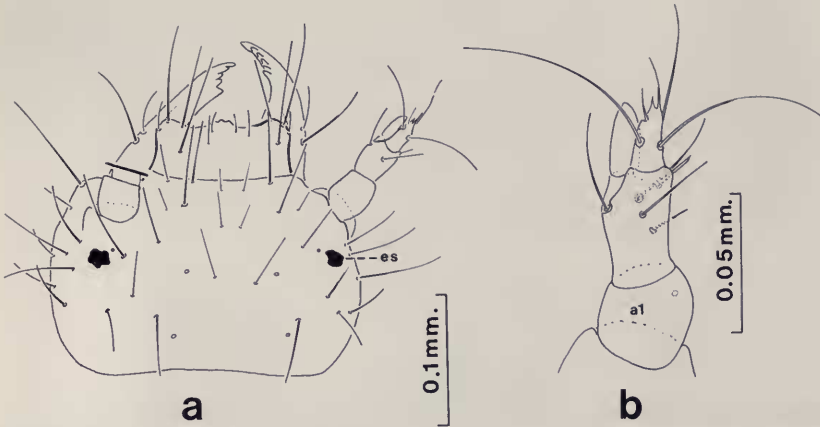


FIG. 6. *Nossidium* (s.l.) sp. (Panama) larva: a, dorsal aspect of head capsule showing eye spots (left antenna partly omitted, maxillae not shown); b, right antenna enlarged, dorsal aspect.

Island, Canal Zone, Panama by John F. Lawrence and received through Dr. A. Newton.

Remarks. — This is the only known Ptiliidae larva so far with any indications of ocelli or pigmented eyespots. It was called to my attention by Dr. A. Newton. The retention of eye pigment in a member of the most generalized group of Ptiliidae represents a plesiomorphic or ancestral character that has been lost in the other genera studied. The associated imago of the Panama larva differs from *Nossidium americanum* in having the median portion of the mesosternum elevated into a triangular area with apex directed anteriorly (the median area in *americanum* is tumid but not sharply elevated or delimited), the mesocoxae are more widely separated, and the pronotal margin is differently grooved. The Panama form therefore probably represents a distinct (undescribed) genus. An undescribed species in the Field Museum collection that probably belongs to the same genus as the Barro Colorado Island form was collected at 7,600 ft. elevation on the Volcan Chiriqui in Panama on the Costa Rica border.

The three pairs of “pores” on the dorsum of the head capsule of the larva are not easy to detect in ordinary slide preparations. They occur, however, in very similar configuration, in *Nephanes titan* (Newm.) which is in the Acrotrichinae, a specialized subfamily of Ptiliidae. They will therefore probably be found in other members of the family as well as related families in the “leptinid series.”

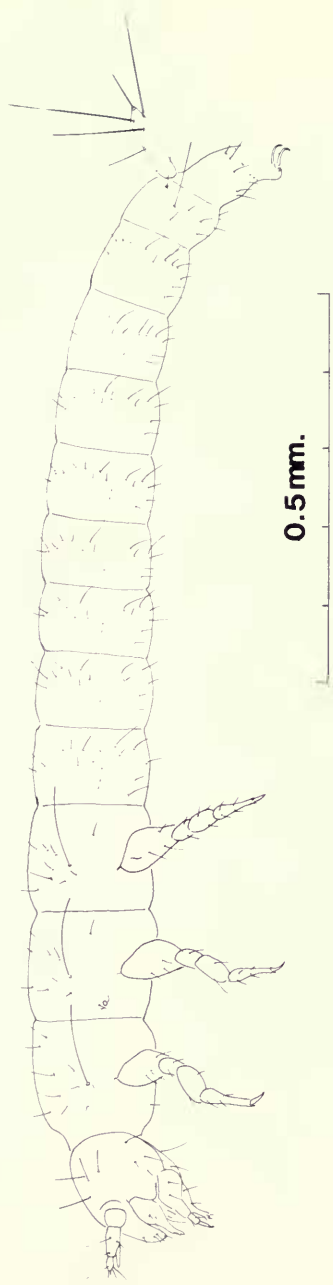


FIG. 7. *Pteryx* sp., late-instar larva, lateral aspect, setal pattern approximate.

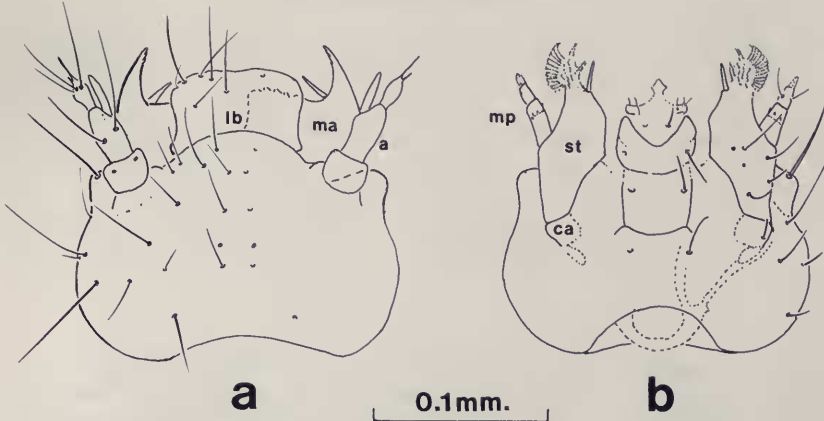


FIG. 8. *Pteryx* sp., larva, head capsule: a, dorsal aspect; b, ventral aspect, mandibles, labrum, and antennae not shown, labial palpi incomplete.

***Pteryx* sp. Figures 7-10.**

Late-instar larva, length 1.5 mm.; width across metathorax 0.17 mm. Similar in general appearance to *Nossidium* but more linear (fig. 7). Differs from *Nossidium* in form of labrum (figs. 8a, 9b), in the proportions of the antennal segments, particularly segment 2 and its sensory appendage (fig. 9a), the more slender apical part

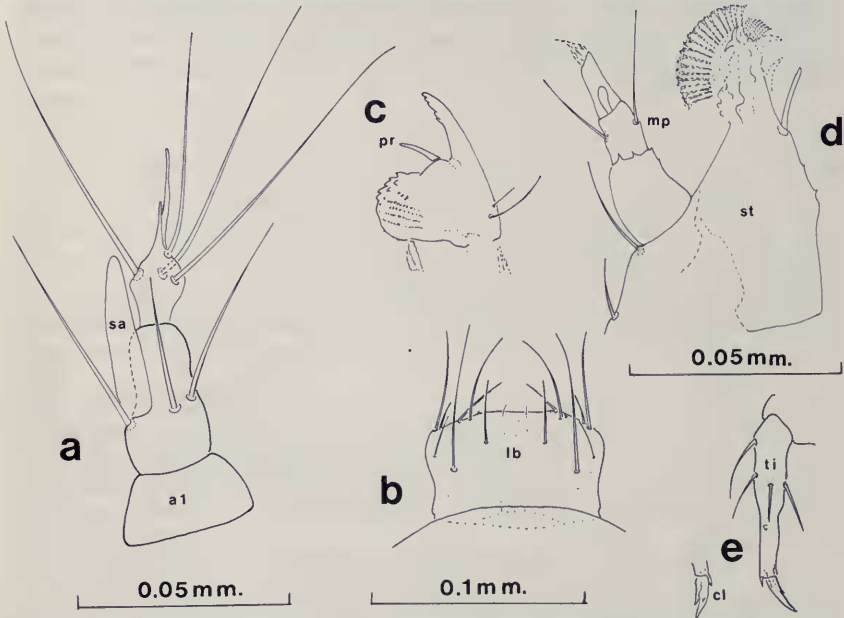


FIG. 9. *Pteryx* sp., larva: a, left antenna, ventral aspect; b, labrum; c, right mandible, dorsal aspect; d, left maxilla, dorsal aspect; e, tibia and claw of third leg.

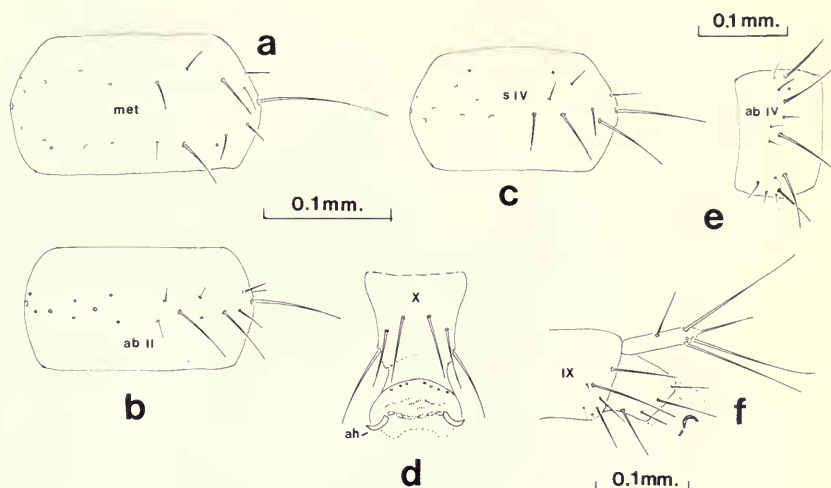


FIG. 10. *Pteryx* sp., larva: a, dorsum of metathorax, showing pattern of setae; b, dorsum of abdominal segment II (a different specimen from a); c, sternum of abdominal segment IV; d, abdominal segment X and anal vesicle (ventral aspect) showing pair of anal hooks and connecting elements; e, lateral aspect of abdominal segment IV (anterior is to the left). Note that a spiracle is lacking; the small opening dorsally is probably a gland as in *Nossidium*. f, end of abdomen, lateral aspect, showing urogomphus and segments IX and X and anal vesicle with anal hook. (a-d and e-f to different scales as shown).

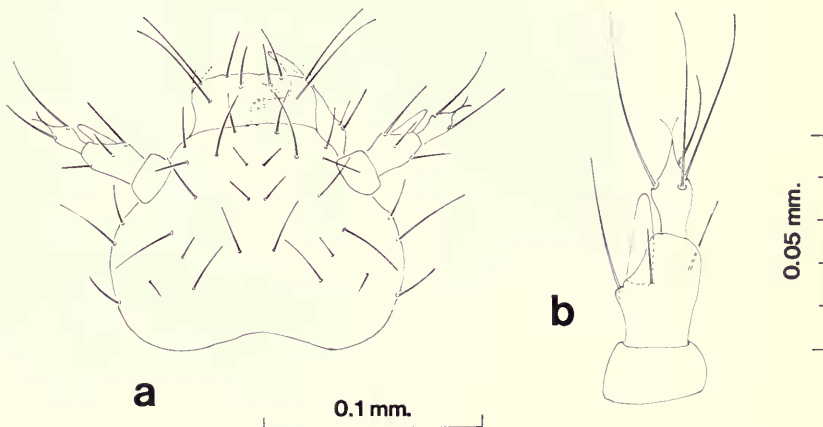


FIG. 11. *Ptinella* sp. (Illinois), larva: a, dorsal aspect of head capsule; b, right antenna, dorsal aspect.

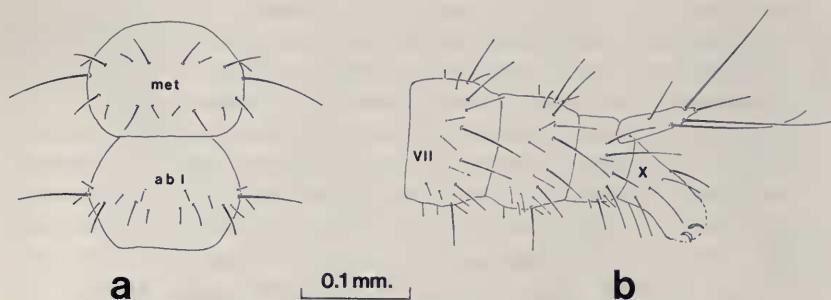


FIG. 12. *Ptinella* sp., larva: a, dorsum of metathorax and first abdominal segment showing pattern of setae; b, lateral aspect of apex of abdomen (segments VII-X) showing setal pattern, form of urogomphus, and terminal anal hooks in anal vesicle of segment X.

of the mandible (fig. 9c), the shape of the urogomphus (fig. 10f), in the absence of detectable spiracles on abdominal segments I-VIII, and in the setal pattern of the head capsule (fig. 8a), and other characters.

Material examined.—More than 100 larvae associated with about 400 *Pteryx* imagos, all apparently of one species, collected July 21, 1967 in Oconee State Park, Oconee County, South Carolina, by S. Peck and A. Fiske. The series was extracted from "log litter" by means of a Berlese funnel. No imagos of other genera of Ptiliidae were in the sample.

Remarks.—There are at least 10-12 species of *Pteryx* from the United States represented in the Field Museum collection. Pending revision, the imagos associated with the larvae described in this paper are designated *Pteryx* sp. 1A. This species is widely distributed in the eastern United States, west to Minnesota, and south to Georgia; it occurs in microhabitats such as forest floor litter and old logs, and is particularly abundant in sawdust piles left from sawmill activities in the woods.

***Ptinella* sp. Figures 11-12.**

Late-instar larva, length 1.32 mm.; width across metathorax 0.16 mm. Similar to *Pteryx* sp. in general appearance and setal arrangement.

Antenna with second segment shorter than in *Pteryx* sp. and with sensory appendage also shorter (fig. 11b). Setal pattern of metanotum and abdominal tergum 1 as in Figure 12a.

Urogomphus (fig. 12b) 1-segmented, similar in form to *Pteryx* sp.

Material examined.—About 20 larvae associated with about 85 *Ptinella* sp. imagos, collected June 20, 1944 in Western Springs, Cook County, Illinois by H. Dybas, "under bark of oak log."

Remarks.—The larva of *Ptinella* sp. (Illinois) is very similar to that of *Pteryx* sp. (South Carolina), differing only in details, such as the shorter second antennal segment and hyaline vesicle. The two genera are also closely related in their adult characters.

The larva of *Ptinella aptera* Guerin from Europe was previously described by Paulian (1941). His larva differs from the one described here, according to his description and figures, in several particulars: the head has epicranial lines, the setal pattern and length of setae is different, and the urogomphus has two segments, the second terminal and very small. Only three setae (instead of 5) are shown. I have not seen epicranial lines nor a second segment of the urogomphus in any Ptiliidae larvae and therefore conclude that these features and the other differences in Paulian's description are the result of errors of interpretation and illustration. The larvae are so minute and delicate that it is quite easy to make such misinterpretations.

Actidium sp. Figures 13-15.

Late-instar larva, length 1.2 mm.; width, across metathorax 0.22 mm. Similar in appearance to *Nossidium* but more linear. Shape and chaetotaxy of head capsule as in Figure 13a. Ventral aspect of head capsule as in Figure 13b; last segment of maxillary palpus slender, much longer than penultimate segment. Segments 2 and 3 of antenna and terminal style (fig. 14a) more elongate than in *Nossidium*; sensory appendage bifurcate, the two arms long and slender. Labrum shallowly emarginate at middle, setae as in Figure 14c. Setal patterns of metanotum and abdominal tergum 1 as in Figure 15a; that of sternum 4 as in Figure 15c. The lateral aspect of the abdominal segments similar to segment IV (fig. 15b); no spiracles detectable, tergal margin not distinct. Urogomphus as in Figure 15d (lateral aspect) and 15e (dorsal aspect). Segment X (fig. 15d) with a membranous anal vesicle, which bears a pair of 'anal hooks.'

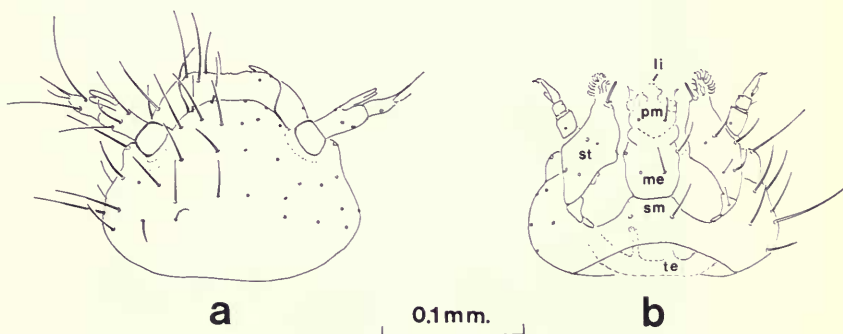


FIG. 13. *Actidium* sp., mature larva, head capsule: a, dorsal aspect; b, ventral aspect, mandibles, antennae, and labrum not shown.

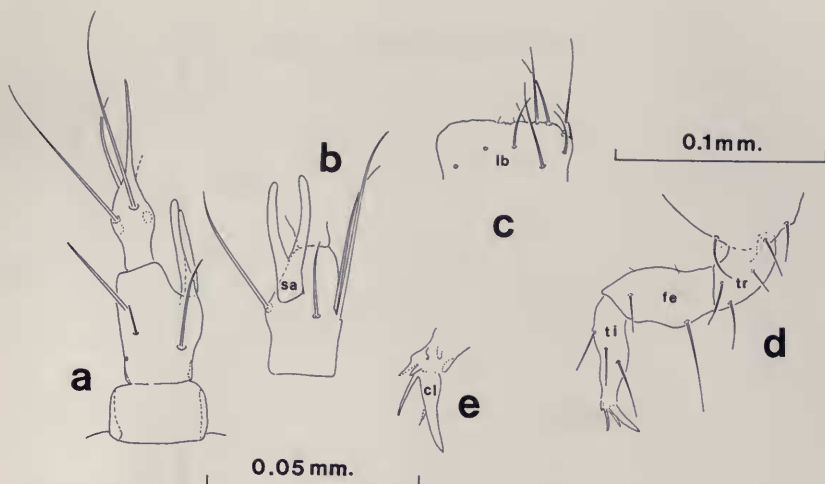


FIG. 14. *Actidium* sp., larva: a, antenna; b, second segment of antenna, from oblique view, showing the bifurcate sensory appendage; c, labrum; d, right anterior leg; e, apex of tibia and claw.

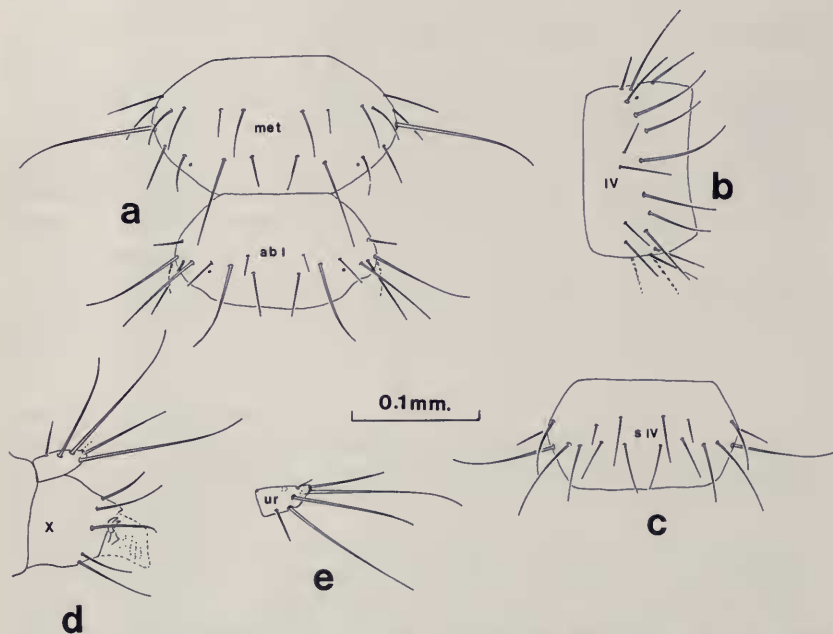


FIG. 15. *Actidium* sp., larva: a, dorsum of metanotum and first abdominal segment, showing setal pattern; b, lateral aspect of abdominal segment IV, showing setal pattern (anterior is to left); c, abdominal sternum 4, showing setal arrangement; d, apex of abdomen, showing urogomphus, segment X, and anal vesicle with retracted anal hooks; e, left urogomphus, dorsal aspect.

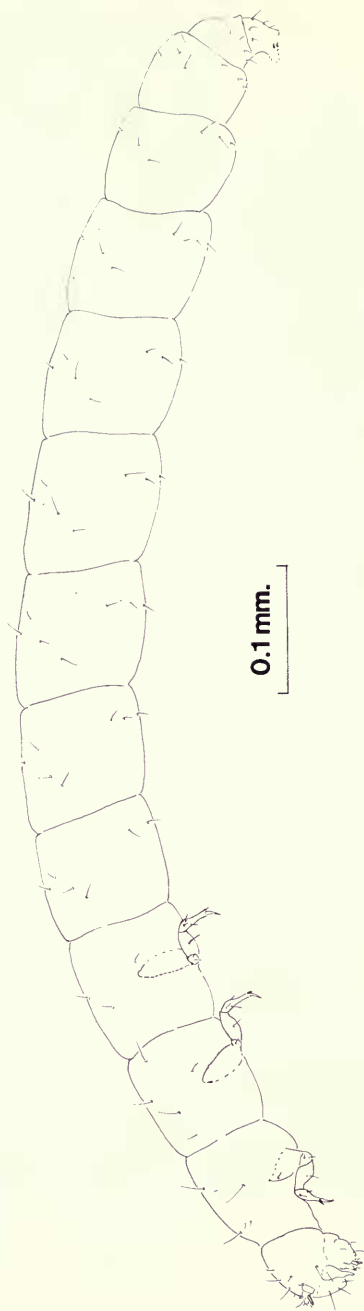


FIG. 16. Late-instar larva of *Nanosella* sp. (Panama). Note the reduction in the size of antennae, legs, and number of setae, and the absence of urogomphi, all of which probably represent an adaptation to life in the cylindrical spore tubes of polypore fungi.

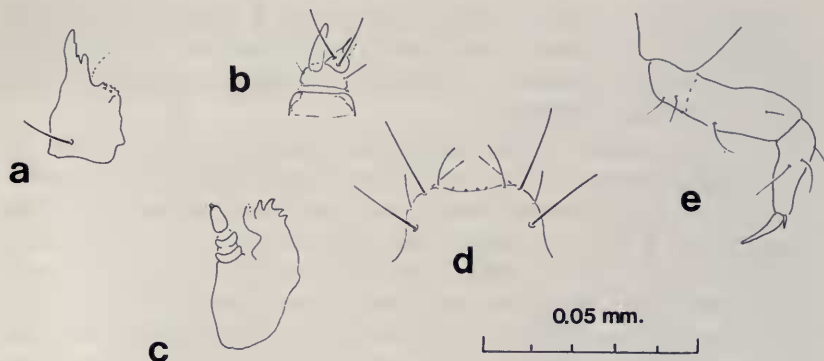


FIG. 17. *Nanosella* sp. (Panama): a, left mandible, dorsal aspect; b, antenna; c, right maxilla, ventral aspect, showing lacinia and 3-segmented palpus; galea lacking?; d, labrum; e, leg.

Leg (fig. 14d) with apical spurs of tibia long, reaching to middle of tarsungulus (fig. 14e).

Material examined.—Many larvae associated with more than 200 imagos of at least two unidentified species of *Actidium*, collected June 18, 1965 at Big Pine Key, Monroe County, Florida, by Walter Suter. The specimens were extracted from brown algae on the beach on the Atlantic Ocean side along with the *Actinopteryx fucicola* larvae described in this paper.

Remarks.—The bifurcate sensory appendage of the antenna readily separates the larvae of this genus from the other genera described here.

Nanosella sp. Figures 16-17.

Late-instar larva (fig. 16). Length 1.08 mm.; width across metathorax 0.10 mm. Body linear, cylindrical in cross-section. Color white. Setae short, and much reduced in number; appendages of head and thorax proportionally short (cf. *Pteryx* sp., fig. 7); urogomphi lacking.

Antennae very short (fig. 17b), segments 1 and 2 transverse; sensory appendage extending beyond apex of segment 3. Mandible as in Figure 17a, prostheca not distinct (lacking?). Labrum as in Figure 17d, with 4 minute denticles on anterior margin at middle. Maxilla as in Figure 17c, galea with prominent teeth, lacinia indistinct in preparation (lacking?). Form and chaetotaxy of legs as in Figure 17e. Urogomphi absent. Anal vesicle of abdominal segment X with a pair of much reduced anal hooks.

Material examined.—Several specimens from a series of about 90 larvae associated with 78 imagos of *Nanosella* sp. Collected March

8, 1959 at Cerro Punta, Chiriqui Province, Panama at 5,600 ft. elevation by H. S. Dybas. Both adults and larvae were in the spore tubes on the under surface of *Fomes melanodermus* (Mont.) Cke. (det. J. Stevenson 1960-1961).

Remarks. — Barber (1924) erected the subfamily Nanosellinae for *Mycophagus* Forster (= *Nanosella* Mots.?) and some related genera of tiny featherwing beetles that live on the under surface and in the spore tubes of polypore fungi (see Dybas, 1961). The subfamily characters mentioned by Barber were not well chosen; they do not, in fact, serve to distinguish the group from other Ptiliidae. However, there are characters such as the form of the mesosternum and the presence of metasternal carinae ("lines") which indicate that the genera form a natural group (or possibly two groups) related to *Ptilium*, *Micridium*, and allied genera that are now included in the heterogeneous subfamily Ptiliinae. Pending a revised classification based on a larger representation of genera from different geographic regions, I regard the genera as forming a group of tribal rank in the Ptiliinae, but am not at present giving the group formal nomenclatural status.

In addition to the larvae of *Nanosella* and of *Throscopitium* (description follows), I have examined the larvae of *Cylindrosella* n. sp. from Illinois. These larvae also lack urogomphi and they have very short antennae and other appendages. These reductions no doubt represent adaptations to life in the narrow, cylindrical spore tubes of their host fungi.

Barber (1924) illustrated a "probable" larva of *Cylindrosella* which possesses eyes, immovable urogomphi, and other characters not found in Ptiliidae; it very probably represents a larva of some genus of Staphylinidae. Paulian (1941) has partially described and illustrated larvae of *Mycophagus* sp. and *Cylindrosella* sp. from Costa Rica. There are a number of discrepancies between those descriptions and that of *Nanosella* in the present study which probably represent differences in observation and interpretation. Paulian's description of the maxilla of *Mycophagus* sp., though, is certainly in error in that there is only one lobe which, moreover, bears spines, and does not have the denticles or curved hooks that are characteristic of the lacinia of all Ptiliidae. It must belong to some other family in the Staphylinioidea.

The prostheca of the mandible is indistinct in the preparations from which Figure 17a was drawn. However, it clearly is present in *Cylindrosella* n. sp. from Illinois.

Parke County, Indiana by H. S. Dybas. The imagos were found on the under surface of *Phellinus gilvus* (Schweinitz) Patouillard (formerly listed as *Polyporus gilvus*).

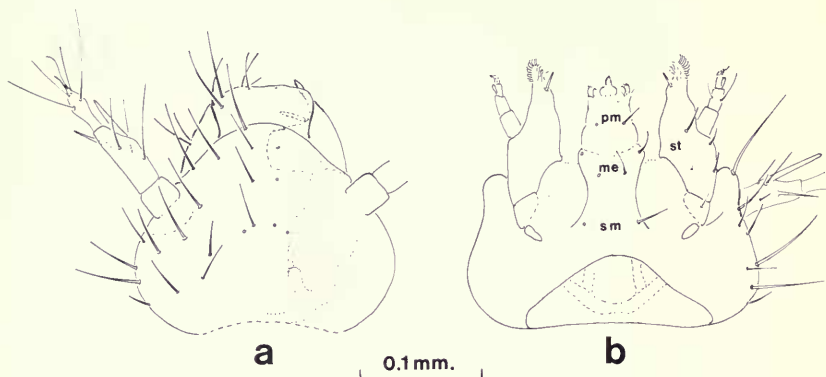


FIG. 19. *Actinopteryx fucicola* Allib., late-instar larva, head capsule: a, dorsal aspect; b, ventral aspect, mandibles and labrum not shown.

Remarks. — The larvae live in the spore tubes of fresh specimens of the host fungus. When the fungus is picked off the tree and handled, the larvae leave their tubes and cross the under surface of the fungus (their white bodies contrasting with the dark yellow brown under surface) and crawl into other spore tubes. They appear to position themselves head-first in the spore tubes and the restriction of the yellow pigmentation to the apex of the abdomen suggests that they normally rest in this position, with the apex of the abdomen at or near the open end of the spore tube.

The adults crawl about actively on the under and upper surfaces of the fungus and hide in crevices in the surface. Unlike *Nanosella* and allies, adults of this genus do not crawl into the spore tubes — they are too broad to fit into tubes of this diameter. *Throscoptilium* and allied undescribed genera differ from *Nanosella* and its allies in structure as well. The most conspicuous difference is in the shape of the sharply defined median elevation of the mesosternum. In *Nanosella* and allies the narrowed apparent apex of the elevation is directed posteriorly between the mesocoxae, whereas in the *Throscoptilium* group of forms the apex of the elevation is directed anteriorly.

The digestive tract of the three larvae studied on microscope slides contained no fungus spores or other identifiable material.

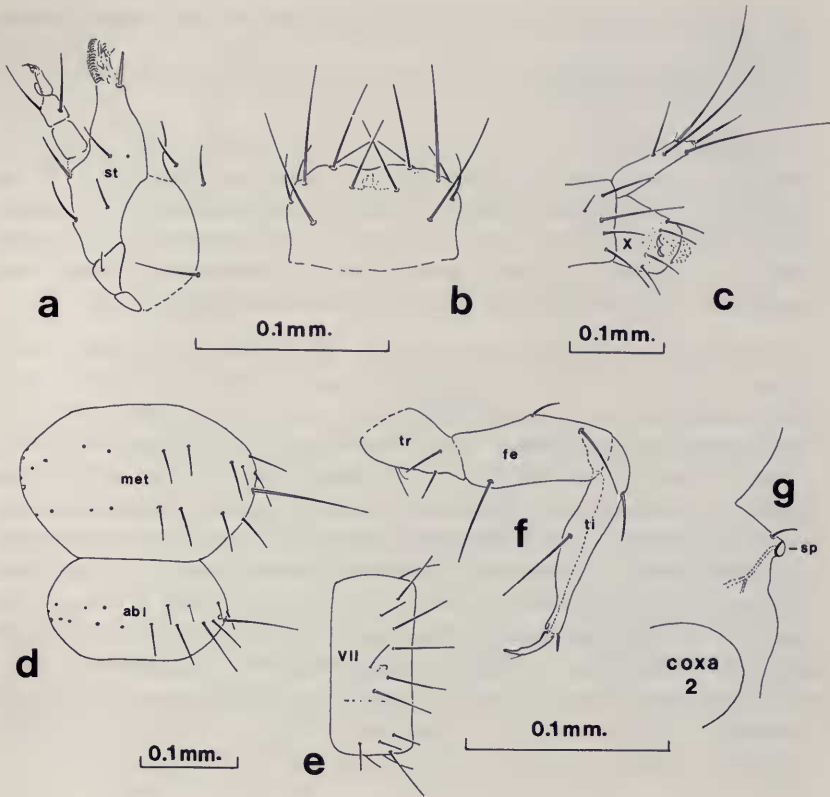


FIG. 20. *Actinopteryx fucicola* Allib., larva: a, maxilla; b, labrum; c, apex of abdomen, showing segments IX and X, urogomphus, and anal hooks of anal vesicle (partly retracted inside segment X); d, dorsum of metanotum and abdominal segment I, showing setal pattern; e, lateral aspect of abdominal segment VII, showing setal pattern. The spiracle is indicated indistinctly at about the middle. f, third right leg, posterior face; g, left thoracic spiracle, anterior to coxa 2, seen from beneath.

Actinopteryx fucicola Allib. Figures 19-20.

Late-instar larva, length 1.5 mm.; width across metathorax 0.28 mm. Similar in general appearance to larva of *Nossidium americanum* Mots., but more slender. Shape and chaetotaxy of head capsule as in Figure 19a. Segments 2 and 3 of antennae (fig. 19a) much more elongate than in *Nossidium*; sensory appendage long and slender, reaching middle of segment 3. Last segment of maxillary palpus (fig. 20a) about equal to penultimate (much longer in *Nossidium*). Labrum (fig. 20b) shallowly emarginate at apex, not produced at middle as in *Nossidium*. Urogomphi more slender (fig. 20c). Setal patterns of metanotum and abdominal tergum 1 as in Figure 20d. The lateral aspect of all the abdominal segments similar to that of segment VII (fig. 20e) which shows an indistinct spiracle and a vaguely delimited tergal

area. The 10th segment as usual bears a membranous anal vesicle with a pair of anal hooks.

Legs slender, tibia (fig. 20f) more than 4 times as long as tarsungulus (less than twice as long in *Nossidium*).

Material examined.—Many larvae associated with about 51 imagos of *Actinopteryx fucicola* Allib. collected June 18, 1965 at Big Pine Key, Monroe County, Florida, by Walter Suter. The specimens were extracted from brown algae on the beach on the Atlantic Ocean side. There were also more than 200 imagos of at least two species of *Actidium* present, and numerous associated larvae.

Remarks.—*Actinopteryx fucicola* Allib. was described from France and it has a wide distribution on the sea coasts of Europe and North Africa as well as the east coast of the United States. I have compared specimens from Florida with European specimens (France) and can find no differences externally or in the form of the female spermatheca. This genus occurs in piles of decaying kelp tossed by storms above the tide line on beaches of the sea shore. At times *fucicola*, both adults and larvae, can occur in large numbers in such situations. It also occurs on the mud among mangroves. Its distribution on both sides of the Atlantic Ocean may be natural and not due to the agency of man. The same habitat (piles of kelp) on the west coast of the United States and Mexico is occupied by *Motschulskium sinuatocolle* Matth., which is not at all related to *Actinopteryx* but belongs to the *Nossidium* group.

Acrotrichis sp. Figures 21-23.

Late-instar larva, length 1.8 mm.; width across metathorax 0.24 mm. Similar in general body form to *Pteryx* (fig. 7). Shape and setal pattern of head capsule as in Figure 21a. Ventral aspect of head as in Figure 21b, last segment (3) of maxillary palpus slender, about as long as previous segment (2). Antenna as in Figure 22a, sensory appendage slender, reaching to middle of segment 3. Labrum as in Figure 22b, with 14 setae. Mandible as in Figure 22c. Terga of thoracic segments indistinctly defined laterally. Dorsal setal pattern of metanotum and first abdominal segment as in Figure 23a. Form and chaetotaxy of legs as in Figure 22d. Urogomphi as in Figure 23c. Anal vesicle of abdominal segment X with 2 well-developed anal hooks (fig. 23c).

Material examined.—Several specimens from a series of more than 100 larvae associated with about a thousand imagos of *Acrotrichis* sp. Collected June 1, 1957 at Dixie Pass, Blue Mountains, alt. ca. 5,000 ft., east of Prairie City, Grant County, Oregon by H.S. Dybas. The adults and larvae were obtained by means of a Berlese funnel from garbage and sublitter in a forest camp.

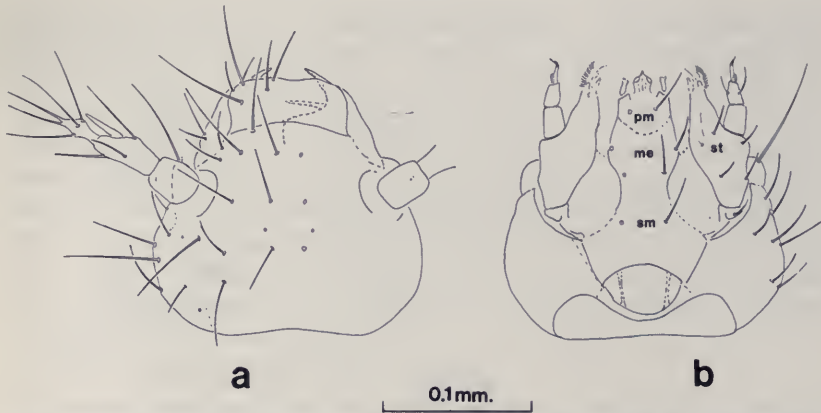


FIG. 21. *Acrotrichis* sp. (Oregon), late-instar larva, head capsule: a, dorsal aspect; b, ventral aspect (mandibles, antennae, and labrum not shown).

Remarks.—Hinton (1941) has described the larva of *Acrotrichis fascicularis* (Herbst) which resembles the Oregon *Acrotrichis* larva in most respects, but there are apparent differences in several features. An additional basal division of the maxillary palpus is described and illustrated by Hinton, thus making the palpus apparently 4-segmented. In the Oregon series this basal division is not clearly separated from the head capsule and I am interpreting it as

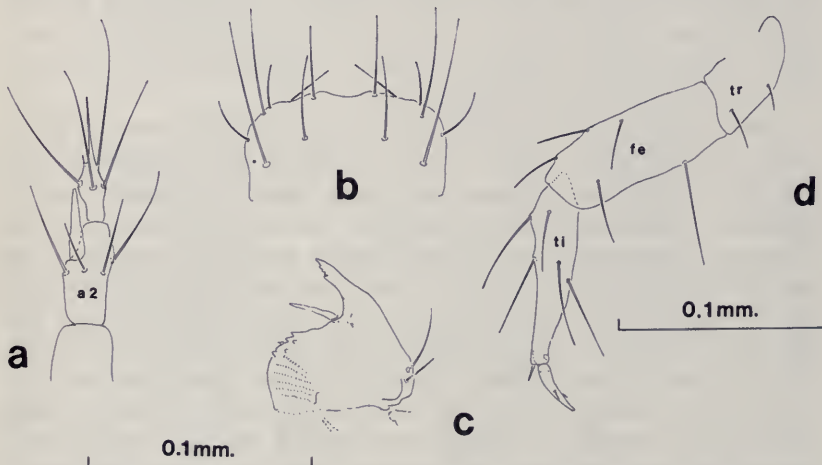


FIG. 22. *Acrotrichis* sp. (Oregon), late-instar larva: a, left antenna, ventral aspect; b, labrum; c, right mandible, dorsal aspect; d, third left leg, posterior face (coxa omitted).

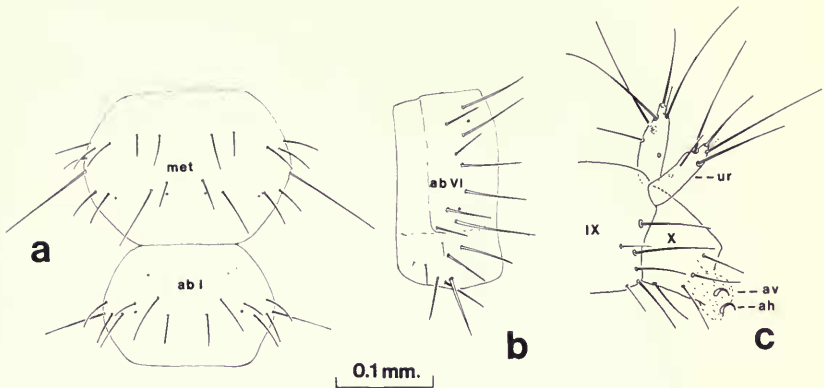


FIG. 23. *Acrotrichis* sp. (Oregon), late-instar larva: a, dorsum of metathorax and first abdominal segment showing pattern of setae; b, abdominal segment VI, left lateral aspect, showing spiracle(?) and setal pattern (anterior is to left); c, apex of abdomen, lateral aspect, showing urogomphus, segment X, and anal vesicle with retracted anal hooks.

representing a palpifer and not a distinct segment of the palpus. Therefore the maxillary palpus of *Acrotrichis* is considered to be 3-segmented as in the other genera studied. The third palpal segment is slender and has a digitiform organ at base and is terminated by a pointed tuft. The terminal (3rd) segment of the antenna is produced into a long, setiform style which is interpreted by Hinton (and illustrated in his fig. 1) as a long seta. The 3rd antennal segment is produced to a greater or lesser extent as an acute style in all the other genera of Ptiliidae studied.

Paulian (1941) has described and illustrated the larva of *Acrotrichis grandicollis* (Mann.). He describes and illustrates the maxillary palpus as 4-segmented, interpreting the terminal tuft of segment 3 as an additional segment. Paulian also describes and illustrates epicranial lines on the dorsum of the head capsule. As stated in the family diagnosis, I have not seen distinct epicranial and frontal lines on the head capsule of Ptiliidae larvae, but one Oregon *Acrotrichis* larva had these lines faintly indicated by thinner portions of the cuticle. Finally, Paulian describes the urogomphus as having a very short second segment that bears a long apical seta. I have not detected a second segment in the urogomphus of any Ptiliidae and consider this a misinterpretation of the socket and base of the apical seta of the urogomphus.

Hinton (1941) also briefly discussed the larva of *Acrotrichis grandicollis* (Mannh.) and stated "it may at once be distinguished

from *A. fascicularis* by lacking urogomphi." The two larvae examined by Hinton were received from F. van Emden and were collected in Belgium: Rochefort, Grotte de Tridaine, 4:IX:1935 (R. Leruth). These same two larvae, or two from the same series, are mentioned by Paulian (1941) as identical in all points with his preceding description of *A. grandicollis* (Mannh.) in which urogomphi were described. Therefore, the urogomphi in the larvae examined by Hinton had been present but had broken off prior to his examination. When urogomphi in Ptiliidae larvae are broken off it is extremely difficult to detect evidence as to where they were attached to the ninth abdominal segment.

***Nephanes titan* (Newm.). Figures 24-25.**

Late-instar larva, length 1.35 mm.; width across metathorax 0.16 mm. Similar in body form to *Pteryx* and *Acrotrichis*. Shape and setal pattern of dorsum of head capsule as in Figure 24a. Ventral aspect of head capsule as in Figure 24b. Antenna as in Figure 24d, sensory appendage slender, reaching to middle of segment 3. Labrum as in Figure 24c, with 12 prominent setae and 2 minute setae on anterior margin near middle. Setal pattern of pro-, meso-, metanotum, and tergum of abdominal segment 1 as in Figure 25a, b. Lateral aspect of abdominal segment IV, showing spiracle and setal arrangement as in Figure 25c. Form and chaetotaxy of leg as in Figure 25d. Urogomphi and last 2 abdominal segments (IX and X), including anal vesicle and 2 retractile anal hooks, as in Figure 25e.

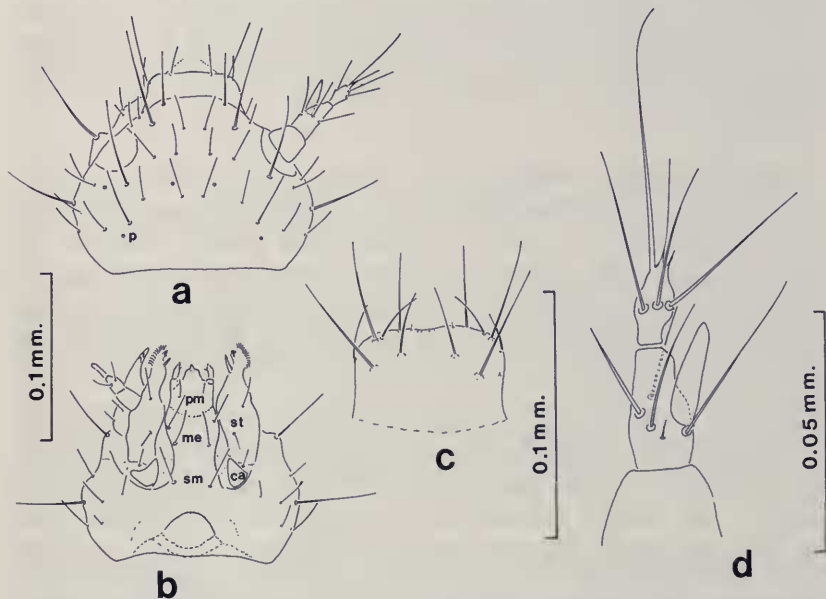


FIG. 24. *Nephanes titan* Newm., late-instar larva; a, head capsule, dorsal aspect; b, head capsule, ventral aspect; c, labrum; d, right antenna, ventral aspect.

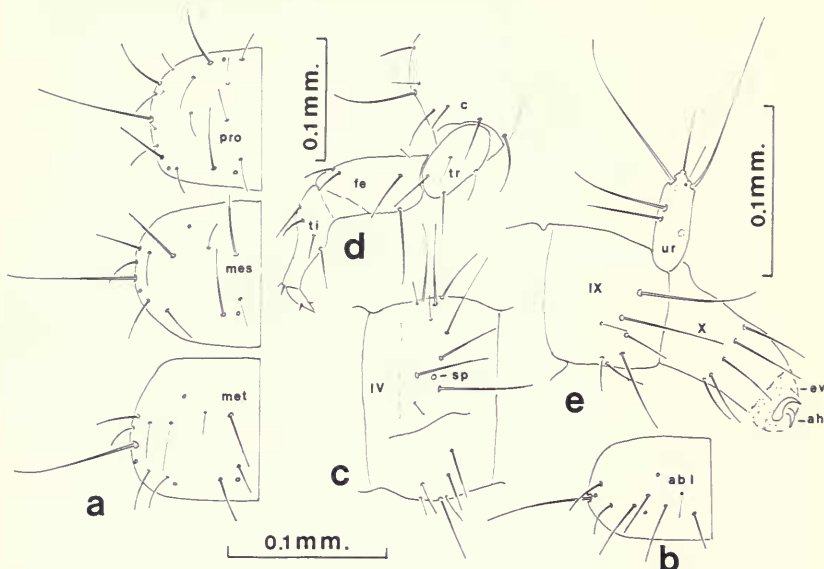


FIG. 25. *Nephantes titan* Newm., larva: a, dorsum of pro-, meso-, and metathorax, showing setal pattern and distribution of "pores"; b, same, 1st abdominal segment; c, lateral aspect of 4th abdominal segment; d, right posterior leg, anterior face; e, apex of abdomen, lateral aspect, showing segments IX and X, one-segmented urogomphi, and membranous anal vesicle containing 2 anal hooks. (figs. a, b, c to same scale.)

Material examined.—Several larvae from a large series of more than 100 larvae associated with 100 plus imagoes of *Nephantes titan*. Collected January 19, 1971 in Skokie, Cook County, Illinois, by John A. Wagner. The larvae and associated adults were collected by means of a Berlese funnel from horse-manure mixed with straw and sawdust (stable sweepings) from the Peebles Stables. *Nephantes titan* has been collected from this stable from 1967 to 1974.

Remarks.—*Nephantes*, along with *Acrotrichis*, is in the subfamily Acrotrichinae in a restricted sense (Dybas, in prep.). The larvae of the two genera are similar in general but differ in a number of respects: the sensory appendage is proportionally less slender and the Xth abdominal segment longer in *Nephantes*. There are also slight differences in the setae of the labrum, leg proportions, and urogomphi. At this time it is not possible to state whether these represent species or generic differences.

Nephanes titan was described from Europe where it is widespread and where it is associated with cow and horse manure (Besuchet, 1971). It has not been previously recorded from the United States, but is abundant in stable sweepings and manure, and in wet compost. There are at least three additional species of *Nephanes* in my material from Florida, Mexico, Brazil, and other areas in the New World, that are closely related to *titan*. In addition, there are other forms from the United States and the Neotropics that resemble *Nephanes titan* but that lack the abrupt apical constriction on antennal segments 6-8, and whose spermathecae do not have the spiral form of *titan*. This opens the possibility that *titan* Newm. may be of American origin and may be an early introduction in Europe. However, the Old World tropical ptiliid fauna is so poorly known, that it is premature to discuss centers of origin or faunal relationships at present.

FAMILY LIMULODIDAE

Diagnosis.—A characterization of the family Limulodidae on the basis of larval features must be highly tentative since it rests only on the following description of *Limulodes parki* Seevers and Dybas. The larva resembles that of the Ptiliidae except for 1) the apparent loss of the 2 anal hooks in the membranous anal vesicle of abdominal segment X; 2) the absence of the terminal tuft of the 3rd segment of the maxillary palpus; and 3) the presence of 4 obtusely pointed denticles under the anterior margin of the labrum. When other Limulodidae larvae are studied, particularly of specialized genera like *Cephaloplectus*, the diagnosis will very probably have to be revised.

Remarks.—All the Limulodidae are obligate associates of ants. They occur only in the New World and the Australian region. There are five genera and 28 described species. The genus *Limulodes* has six subgenera, some of which will probably be raised to genera when the family is studied more intensively. There are additional undescribed species and genera in the Field Museum collection. For a general account of the classification and biology of the family see Seevers and Dybas (1943).

Limulodes (Neolimulodes) parki Seevers and Dybas. Figures 26-29.

Mature larva (fig. 26), length 1.2 mm.; width across metathorax 0.27 mm. Body linear, very little wider at thorax than abdomen, subcylindrical in cross-section. Color white, becoming very slightly yellow on the head capsule, more especially on



FIG. 26. *Limulodes (Neolimulodes) parki* Seevers and Dybas, (Limulodidae) late-instar larva; lateral aspect.

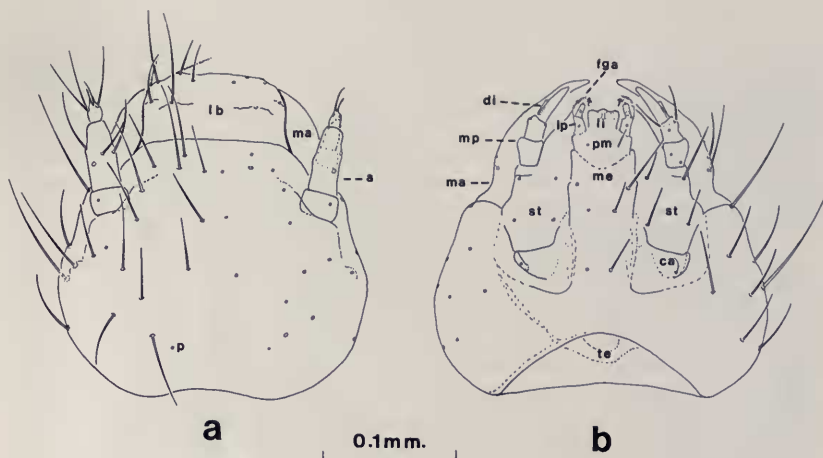


FIG. 27. *Limulodes parki* Seevers and Dybas, (Limulodidae), larva, head capsule: a, dorsal aspect; b, ventral aspect.

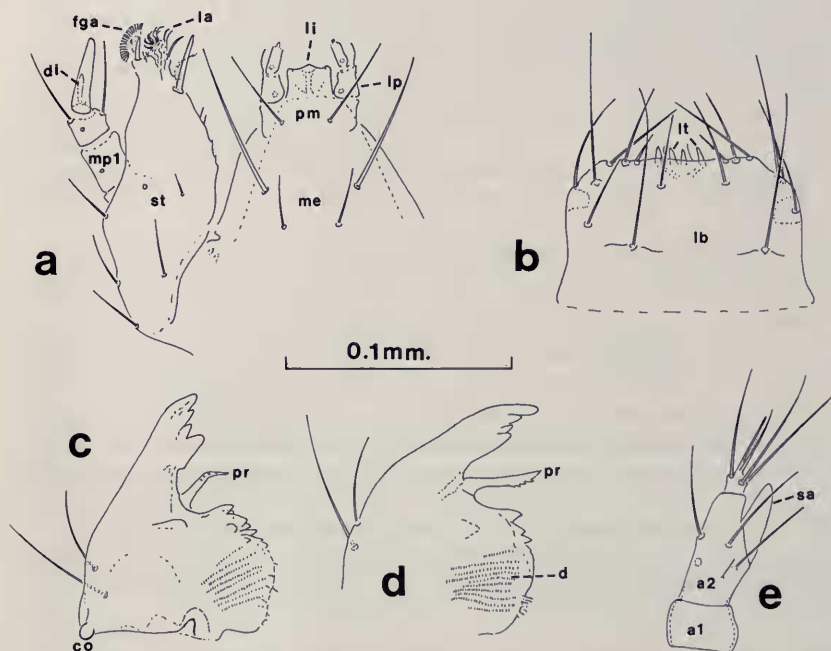


FIG. 28. *Limulodes parki* Seevers and Dybas, (Limulodidae), larva: a, right maxilla and labium, ventral aspect; b, labrum, dorsal aspect; c, right mandible, ventral aspect; d, left mandible, dorsal aspect; e, right antenna, ventral aspect.

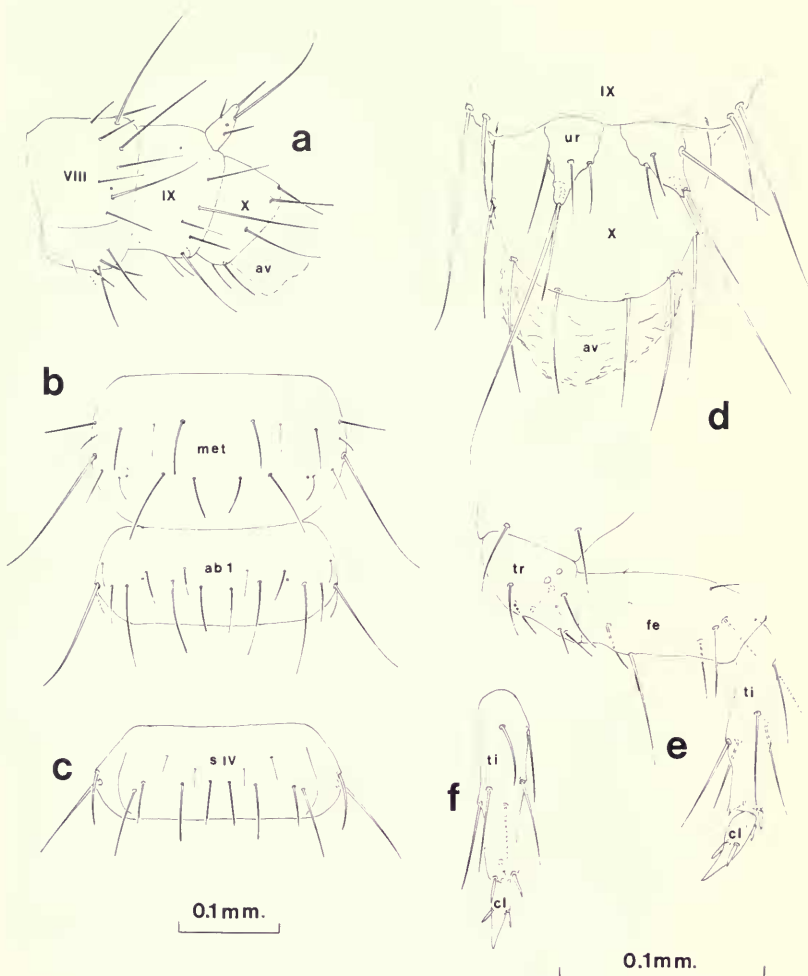


FIG. 29. *Limulodes parki* Seevers and Dybas, (Limulodidae), larva: a, apex of abdomen, lateral aspect, showing segments VIII-X, anal vesicle, and urogomphus; b, dorsum of metathorax and 1st abdominal segment, showing pattern of setae; c, venter of abdominal segment IV; d, abdominal segments IX and X, and part of VIII, dorsal aspect, showing setae, urogomphi, and membranous anal vesicle, in which no anal hooks were detected; e, front leg; f, left anterior tibia and claw, viewed from the front side.

the mandibles. All setae simple, slender, and pointed at apex; no composite setae present.

Head capsule (fig. 27a, b) lightly sclerotized, without epicranial or clypeal sutures; labrum separated by a distinct suture. Ocelli absent. Antennae 3-segmented (fig. 28e) segment 2 more than twice as long as 1 and bearing a stout sensory appendage on the inner side which extends beyond the apex of the segment; segment 3 small, bearing 2(?) long, terminal styles; antennal setae as in Figure 28e. Labrum transverse (fig. 28b), bearing about 16 setae and with 4 obtusely pointed "denticles" extending forward from under the middle of the front margin.

Underside of head with setal arrangement as in Figure 27b. Maxilla as in Figure 28a, second segment of maxillary palpus shorter than 1, third segment long, slender, obtusely pointed, without a terminal 'tuft,' and with thin walled process on the dorsal side arising from the base. Galea fringed; lacinia as indicated in Figure 28a. Mentum and submentum not separated by a distinct transverse suture; labium with 2-segmented palpi, the second narrow, about as long as the first, and bearing a short apical process; ligula well-developed, very slightly produced at middle. Ventral side of head capsule with form and setae as in Figure 27b; gula not defined.

Mandibles (fig. 28c, d) similar in form, the right mandible with the proximal sub-apical tooth more prominently developed than the left mandible.

Thorax a little broader than first abdominal segment, the terga of both thorax and abdomen not clearly defined. Dorsal setae of thorax as in Figure 29b (metanotum). Setal patterns of abdominal segments as in Figure 29b (tergum of segment I), 29c (sternum of segment IV), and 29a (lateral aspect of segments VIII-X, and anal vesicle). Spiracles annular in form, present on sides of abdominal segments I-VIII. Spiracle of mesothorax larger and located as in Figure 26. Urogomphi 1-segmented, form and setae as in Figures 26 and 29a, d. Anal vesicle protrusible; no pair of anal hooks detected in 2 slide-mounted larvae.

Legs all similar in form and setae to anterior leg (fig. 29e); tibia with a pair of apical spines; tarsungulus stout, with a pair of well-developed spines near middle.

Material examined.—Three larvae collected in March-May, 1954, Cook County, Illinois, by Henry S. Dybas and Charles Seevers. The larvae were under a flat limestone rock which covered a colony of *Aphaenogaster rudis* s. l. (det. by W. L. Brown, Jr.). Adult *Limulodes parki* Seevers and Dybas were present among the ants. It was not possible to determine whether the larvae were actually in the galleries or whether they were in the surrounding soil. No other beetle imagoes besides *Limulodes* were present.

Remarks.—Paulian (1941, pp. 274-276) described the putative larva of *Cephaloplectus mus* Mann, which is a highly specialized member of the Limulodidae, on the basis of two larvae collected in a bivouac of *Eciton burchelli*, 25: III: 34, Hamburg Farm, Costa Rica by F. Nevermann. He states "Ces larves ont été indentifiées *ex societate imaginis*; l'originalité de leurs caractères vient confirmer cette identification." The Costa Rica larva, judging by the description and figures, clearly is not in the "leptinid series" of

Böving and Craighead. It is about 8.5 mm. in length and falls into the specialized staphylinoid series. The mandibles lack a mola and a prostheca; the maxillae are very different: the mala is not divided into a lacinia and galea. The figure of the head (fig. 1122, p. 275) shows epicranial and clypeal sutures, and there is a single large pale ocellus (?) on each side. Judging by the morphology of the adults, Limulodidae larvae should be quite similar to Ptiliidae larvae, though *Cephaloplectus* larvae could conceivably be quite specialized in some respects, since the adults are highly specialized Limulodidae. In Kasule's 1966 key to subfamilies of Staphylinidae (and related families), the characters of Paulian's larva point to Staphylinidae, though the subfamily is not certain. It may possibly belong to the Aleocharinae.

The "teeth" of the labrum in the larva of *Limulodes* are directed ventrally from the plane of the labrum and are clearly not socketed and thus are not similar to the conical pegs in this position in the Catopinae: Bathysciini (Deleurance-Glacon, 1963). The maxillary palpus has a distinct sclerotization at its base that I am interpreting as a palpifer. The apex of the last palpal segment lacks the tufted process of *Nossidium* and the other genera described here; it may possibly bear a minute inserted sensillum but this cannot be determined in my preparations.

The gut of one larva was packed with indeterminate matter, and there were small soil particles (crystalline fragments) intermixed. The adults are reported to feed (Park, 1933) by scraping oils and other materials from the integument of the host ant larvae, pupae, and even the workers.

DISCUSSION

Ptiliidae are currently classified into three subfamilies or major groups: Ptiliinae (Ptiliini), Nanosellinae, and Acrotrichinae (Acrotrichini). The Limulodinae (Ganglbauer, 1899) formerly in the Ptiliidae, were removed and combined with Staphylinidae: Cephaloplectinae (pars) by Seevers and Dybas (1943) to form the Limulodidae. The Acrotrichinae include the genera with more or less truncate elytra, whereas the Ptiliinae include all the genera with complete elytra, except for *Nanosella* and allies from fungus spore-tubes, for which Barber (1924) erected the subfamily Nanosellinae.

This formal classification is quite artificial — long ago, Flach (1889) recognized, for example, that the genera with truncate elytra

did not constitute a natural group. And the group with complete elytra (Ptiliinae) includes a number of very diverse types. While the phylogenetic relationships in the Ptiliidae are still very incompletely understood, it is clear that the most generalized Ptiliidae, on the basis of adult structure, are *Nossidium* and its allies (unpublished data). In the *Nossidium* group, the elytra are complete and not truncate and the abdomen has 10 external segments. The meta-thoracic wings do not have the extreme "featherwing" structure that is characteristic of the other Ptiliidae — there are two basal struts, not one; the membrane is relatively broad, the marginal hairs relatively short; and the wing-folding pattern has longitudinal as well as transverse folds (Forbes, 1926). The strigulae of the dorsum of the abdomen (which presumably act as friction pads aiding in wing folding) are diffuse, much as in *Hydraena* (Hydraenidae), and are not concentrated into "fingerprint whorl" patches. The aedeagus consists of a median lobe and also 2 lateral lobes which are lost in most other Ptiliidae. The hind coxae are contiguous. There are a number of additional characters which are in a generalized condition for the family. The *Nossidium* group consequently is a well-defined group of subfamily rank, though I am not giving it formal nomenclatural status at this time. It constitutes the most generalized group of Ptiliidae. In the present study, it is represented by larvae of *Nossidium americanum* Mots. from Illinois, and *Nossidium* (s.l.) species from Panama.

The Acrotrichinae, if *Pteryx*, *Ptinella*, and allies are excluded, represents a distinctive and highly specialized group of Ptiliidae. The abdomen is 9-segmented — the apparent 9th or terminal tergum is formed from terga 9 and 10 which are fused in a characteristic way, the point of fusion being marked by a tooth on each side. The elytra are truncate. The aedeagus is a simple tube with a pair of ventral hooks, and it has a symmetrical shape in the abdomen when viewed from beneath. Unlike the other Ptiliidae, the Acrotrichinae have curious spermatophore-like structures that are produced in the abdomen of the male and transferred to the female spermatheca where they are stored. All the other Ptiliidae as far as is known (unpublished) have free sperm that are deposited in the female bursa and traverse their way up the spermathecal duct to the spermatheca where they are stored. In these, as well as other features, the Acrotrichinae (as restricted here) are a sharply defined and highly specialized group of subfamily rank in the Ptiliidae. In the present study the subfamily is represented by larvae of

Nephanes titan (Newm.) from Illinois, and *Acrotrichis* sp. from Oregon.

The remaining genera of larvae in this study are placed in the very heterogeneous subfamily Ptiliinae for the present, though they represent three or four very distinct lines in the family. *Pteryx* and *Ptinella* are closely related on the basis of adult structure; together with some other described genera (*Ptinellodes*, *Pterycodes*, etc.) and numerous undescribed genera, they form a distinctive group which can be termed the "pterycine group" for the present. They were included in the Acrotrichinae because of their truncate elytra. The hind coxae are usually extremely widely separated, the aedeagus is a simple tube (without lateral lobes) which lies on its side and has an asymmetrical appearance in the abdomen when viewed from beneath. The "meso-metasternal" suture lateral to the mesocoxae is curved anteriorly from the coxa. Polymorphism with respect to the eyes, wings, and body pigmentation is especially common — in *Ptinella*, for example, all the species, in both sexes, occur in a vestigial and a normal morph.

The two genera, *Nanosella* and *Throscoptilium*, belong to a distinctive group whose larvae are specialized for living in the spore tubes of polypore fungi. The larvae can be separated from other Ptiliidae larvae because of reductions or losses (e.g., loss of urogomphi), but the adults are not sufficiently different from some other genera of Ptiliinae to merit their separation as a subfamily (Nanosellinae Barber, 1924) as discussed under the description of the larva.

The genus *Actidium* forms a rather distinctive line, based on adult structure, within the composite Ptiliinae. The larvae differ from all the other known Ptiliidae in the bifurcate condition of the sensory appendage of the antenna.

Actinopteryx is a genus of the marine littoral where it occurs most abundantly in piles of decaying kelp thrown up on the beaches above the tide line by storms. It has the facies of some Acrotrichinae (e.g., *Acrotrichis*). The abdomen is 10-segmented in the female; in the male, the suture between terga 9 and 10 is lacking and the abdomen appears 9-segmented. For the present it must be regarded as a distinct line of uncertain relationships to other Ptiliidae.

The genera of larvae in this study therefore represent five or six distinct lines in the Ptiliidae, as evidenced by the structure of the adults, and include the most generalized Ptiliidae (*Nossidium*), as

well as specialized forms (*Acrotrichis*, *Nephanes*). Therefore, the sample of genera of larvae upon which the family characterization and diagnosis is based represents a broad range of taxa in the Ptiliidae.

The larvae differ among themselves in numerous details such as relative size, shape, and proportions of various structures (antennal segments, sensory appendage, apical styles, maxillary palpi, ligula, lacinia, galea, urogomphi, abdominal segment X, etc.); in features such as presence of eyespots, loss of urogomphi, labrum anteriorly produced at middle; and in details of chaetotaxy. There are so few species described so far that I am deferring the construction of a key or a larval classification within the family. In too many cases one cannot decide at present whether a particular character represents a species difference or whether it is a group character shared by a number of taxa.

CLASSIFICATION OF THE LIMULODIDAE

On the basis of adult structure the two families Ptiliidae and Limulodidae are closely related, although the Limulodidae have many specializations that appear to be adaptations for life in ant societies (Seevers and Dybas, 1943). The specializations are especially striking in derived genera like *Cephaloplectus* that live with the nomadic societies of army ants (*Eciton* and other Dorylinae) in the American tropics.

The most primitive Limulodidae are *Rodwayia* from Australia and "*Limulodes*" *argentinus* Bruch and *elongatus* Bruch, both from southern South America (Argentina). These last two species were described in *Limulodes* but they do not belong to any of the subgenera presently included in that genus. They are more primitive in several respects and one or two new genera will need to be erected for these species. These forms have the general limulodid habitus but the front tibia is unmodified and lacks the outer row of heavy, close-set spines characteristic of all other Limulodidae (except the aberrant *Paralimulodes*). The tibiae are therefore similar to those of many Ptiliidae. The spermatheca in *Rodwayia* is typical of the Ptiliidae in the development of the pump apparatus, which tends to be reduced or lacking in most Limulodidae. In "*Limulodes*" *argentinus*, there is a large flat, unpigmented eye facet on each side of the head capsule, and the pump apparatus is somewhat reduced (its condition in *elongatus* Bruch is not known, since the single specimen examined, a "cotype," is a male). In all the other known

Limulodidae, there is no trace of an eye. *Limulodes* (*Neolimulodes*) *parki* Seevers and Dybas and the other *Limulodes* species described in Seevers and Dybas (1943) are not as primitive as *Rodwayia* and the Argentine "*Limulodes*"; they have well-developed rows of spines on the anterior tibiae; they lack any vestige of an eye; and the pump apparatus on the spermatheca is greatly reduced.

A number of other beetle families in the past, besides the Limulodidae, have been composed entirely of inquilines in ant or termite societies. However, these families have all been subsequently incorporated into other existing families and today the Limulodidae appears to be the only remaining family of beetles still generally recognized that consists entirely of myrmecophiles. Myrmecophiles and other inquilines often develop extreme structural modifications associated with their special habits, and these adaptations have created special problems in placing myrmecophiles into a system of classification (see Lawrence and Reichardt, 1969, for a discussion of this problem). On these grounds and because of the close relationship in many morphological features between the two families, Crowson (*in litt.*) has raised the question whether the Limulodidae should be separated from the Ptiliidae as a distinct family. I am deferring this problem until the phenetics and branching sequence of the higher categories in the Ptiliidae are better understood. For the purposes of this paper the Ptiliidae and Limulodidae are considered to be two separate families that are closely related on the basis of both adult and larval characters.

THE LEPTINID ASSOCIATION OF FAMILIES OF THE STAPHYLINOIDEA

The composition of the Staphylinoidea has varied somewhat over the years, but there are now about 10 families generally included in the superfamily (see, for example, Paulian, 1941; Crowson, 1955). These families are the Leiodidae (=Anisotomidae in the sense of Crowson, 1955; includes Catopidae and Leiodidae), Leptinidae, Ptiliidae, Limulodidae, Hydraenidae, Silphidae, Staphylinidae, Scaphidiidae, Scydmaenidae, and Pselaphidae. The Hydroscaphidae, formerly included in the Staphylinoidea, have been transferred (Crowson, 1955) to the suborder Myxophaga. Crowson (1955) also includes the Dasyceridae in the Staphylinoidea and treats the Micropeplidae as a subfamily of the Staphylinidae, but the status and relationships of these two groups are not well established at present. Finally, the Clambidae have been transferred by Crowson (1960) to the superfamily Eucinetoidae.

The family Hydraenidae is listed in the Hydrophiloidea in most North American classifications (for example, Arnett, 1968). A number of authors, primarily on the basis of larval features, have pointed out the staphylinoid affinities of this family (Forbes, 1926; Böving and Craighead, 1931; Paulian, 1941) and it is listed in the Staphylinidea in most European classifications (see Paulian *in* Grassé, 1949). Böving and Craighead (1931) placed the larvae of the Hydraenidae in the Staphylinidea rather than the Hydrophiloidea because of the form of the maxillary "palpiger" (=palpifer), and the form of the spiracles. According to their classification, the maxillary palpifer in the Staphylinidea is connected to the stipes as a rule and does not often carry a finger-shaped galea; the spiracles are annular. In the Hydrophiloidea, the maxillary palpifer is free and joint-like, and usually carries a finger-shaped galea, and the spiracles are biforous. However, Crowson (1955), after reviewing the staphylinoid features of both adults and larvae, retained the family in the Hydrophiloidea because of the hydrophilid form of the antenna and "general aquatic adaptations" of the adults. Though there has been lack of agreement as to the systematic position of the family Hydraenidae, I regard it as clearly belonging in the Staphylinidea because of the characters of the larva (particularly the maxilla of *Hydraena*) and because of the close resemblance in numerous features of the dorsum of the abdomen of the adult to that of the generalized ptiliid *Nossidium* (unpublished data).

On the basis of adult structure there is no clear and consistent pattern of relationships between the families of the Staphylinidea nor among the subfamilies of the huge and heterogeneous family Staphylinidae. However, some broad groupings or divisions of the superfamily have been proposed. On the basis of larval characters, Böving and Craighead (1931) recognized a "leptinid association" containing "very primitive larvae." In this association, these authors included the Leptinidae, Anisotomidae, Hydraenidae, and Ptiliidae. They regarded the Hydroscaphidae to be closely related to the Hydraenidae. Paulian (1941) recognized the same grouping based on larvae, except that the Anisotomidae (s.l.) are treated by him as two families, the Catopidae and Leiodidae.

Jeannel and Jarrige (1949) followed Paulian's larval treatment and added characters of the aedeagus of the adults to support the division of the Staphylinidea into two main groups of families. In the Catopiaria (corresponding to the Leptinid association) the parameres of the aedeagus are said to be inserted on the dorsal surface of

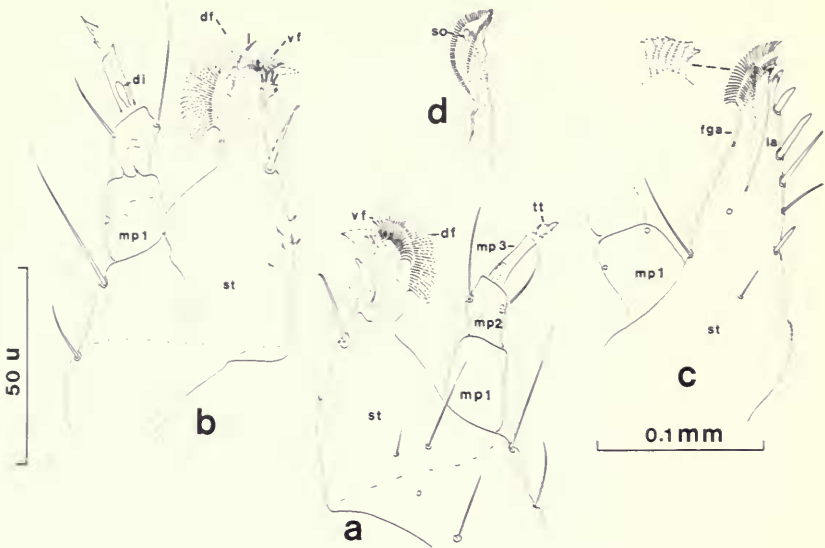


FIG. 30. a, *Pteryx* sp., (Ptiliidae) late-instar larva, maxilla, ventral aspect; b, same, dorsal aspect; c, *Ptomaphagus (Adelops) hirtus* Tellkamp, larva, instar (?), maxilla, dorsal aspect (Leiodidae: Catopinae: Ptomaphagini); d, *Speonomus d. delarouzei* Fairm. (Catopinae: Bathysciini), larva, fimbriate lobe of maxilla (= "galea" auct.) showing "sensory organs" (after S. Deleurance-Glaçon, 1963, pl. IV, fig. 5", $\times 547$).

the median lobe. In the Brachelytra (the remaining families of Staphylinioidea) the parameres are inserted on the ventral surface. These characters require interpretation as to the torsion of the aedeagus in certain lineages, so that the apparent dorsal surface may actually be morphologically the ventral surface.

The larvae of the "Leptinid association" have been distinguished from other Staphylinioidea by the form of the mandible, which has a greatly expanded molar region that is denticulate or asperate. The inner margin usually bears a slender, articulated process (prosthema) just distal to the expanded mola. A similar form of mandible occurs in widely separate groups in the Coleoptera, for example, in the Sphaeriidae (Britton, 1966) and Hydroscaphidae (Böving, 1914) in the suborder Myxophaga, and in the Cucujoidea: Cryptophagidae (see Peterson, 1951, fig. c4, k) in the suborder Polyphaga. Therefore, this form of mandible appears to represent a primitive condition and it appears to be associated with feeding on molds and spores of fungi, on algae, or on soft organic detritus.

The urogomphi are articulated and composed of one or two segments (lost in *Nanosella* and related Ptiliidae that inhabit spore

tubes of fungi). The antennae are 3-segmented and there is a sensory appendage on segment 2.

The maxilla in most members of the leptinid association of larvae is highly distinctive in structure. In *Ptomaphagus* (fig. 30c) which is in the Leiodidae (Catopinae: Ptomaphagini) the stipe of the maxilla is prolonged into a hooked lacinia which bears a subapical tooth and is furnished on its medial or inner margin with several stout spines. Lateral to this and arising from its dorsal surface, is a more lightly sclerotized or membranous lobe which extends beyond the lacinia and which terminates in a fimbriate apex, consisting of a dorsal and a ventral fringe. The individual elements of the dorsal fringe are bifurcate or expanded at their tips. Inside the apex, between the two fringes, are two rounded or oval masses which are continued as stalks or rods inside the galear lobe.

Deleurance-Glaçon (1963) illustrates a fimbriate galea in all of the eight genera of European cave-beetles (Leiodidae: Catopinae: Bathysciini) that are treated in her well-illustrated paper. Figure 30d of *Speonomus d. delarouzei* Fairm., taken from her work, shows a fimbriate lobe in the form of a fringed envelope around two structures (similar to those in *Ptomaphagus*, fig. 30c) which she terms "sensory organs." (She describes the lobe as arising from the ventral face of the maxilla, whereas it appears to arise from the dorsal side in *Ptomaphagus*.)

In a larva of *Leptinus* sp. (Leptinidae) from Florida that I have examined, there is similarly a toothed and spined lacinia and a galear lobe with two apical fringes. Two thin-walled bent sensillae (?) and an indistinct internal mass are associated with the two fringes. In *Leptinillus validus* Horn (Leptinidae) from beaver lodges in Canada, the galea is surmounted by a dense tuft of fine wavy filaments and looks superficially different from *Leptinus* sp. However, a fine fringe of regularly spaced filaments, and two thin-walled sensillae (?) can be detected in the dense tuft. The fringe and two sensillae (?) are not shown in the illustration in Wood, 1964 (fig. 12, p. 39). In the specialized beaver-parasite *Platypsyllus castoris* Ritsema (Leptinidae), the maxillary lobe, according to Wood (1964, fig. 32, p. 54), is reduced to an undivided mala which is densely setose.

Paulian (1941) illustrated a fringed galea in a number of genera of Anisotomidae (=Leiodidae) such as *Anisotoma* (Agathidiini) and *Nargus*, *Choleva*, *Sciodrepes*, and *Catopidius* (Cholevini). He also illustrated a fringed galea in *Ptomaphagus sericatus* (Chaudoir)

(Ptomaphagini), in several other genera of Bathysciini in addition to those treated in Deleurance-Glaçon (1963), and in *Ptinella* and *Acrotrichis* (Ptiliidae). In the present paper, a fimbriate galea is shown to be present in all the genera of Ptiliidae studied, except *Nanosella* and *Throscoptilium*, which are derived forms in a number of respects, such as the loss of the urogomphi. The fimbriate galea also is present in *Limulodes*, the only genus of Limulodidae known as larvae.

In larvae of *Hydraena* sp. (Hydraenidae) from Mt. Ranier, Washington, received from Dr. A. Newton, there is clearly a fimbriate galea (fig. 31). In *Ochthebius* and *Meropathus* though, the galea is fingerlike, judging by the illustrations and descriptions in Böving and Craighead (1931), Paulian (1941), and Beier and Pomeisl (1959). The fingerlike galea in these latter two genera then, is very probably a derived condition in the Hydraenidae.

The fimbriate galea therefore appears to be present, in most members at least, in all the families of the leptinid association. The detailed structure of the fimbriate galea varies, however, within the group. In *Acrotrichis* sp. (Ptiliidae) from Oregon, there seems to be a third apical fringe. In *Nossidium*, the fimbriate galea is clearly separated from the lacinia. In most Ptiliidae, though, the lacinia and galea of the maxillary lobe are united into one structure which seems to be quite complex (fig. 30b). There appear to be associated sensory (?) structures, but the details are not clear in the preparations studied.

The use of the term "galea" in the present paper is only descriptive. As Paulian (1941) points out, the "galea" in the Catopidae (=Leiodidae) is not the same structure as the "galea" in the suborder Adephaga, or in the Staphylininae (suborder Polyphaga: Staphylinidae), for example, *Ocypus olens* Müller (Paulian, 1941, fig. 38).

Ptiliidae larvae are most similar to the Limulodidae, judging by the genus *Limulodes*. That genus differs from the Ptiliidae mainly in the apparent loss of the pair of anal claws or hooks in the anal membrane. There are some other differences, such as the absence in *Limulodes* of the apical (sensory?) tuft of the 3rd segment of the maxillary palpus and the presence of peg-like teeth at the anterior margin of the labrum, but the significance of these differences cannot be assessed at present.

Ptiliidae larvae also resemble those of the Hydraenidae in general appearance, though there are numerous differences. The main dif-

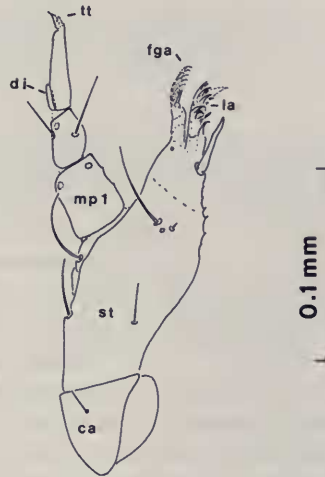


FIG. 31. *Hydraena* sp., (Hydraenidae) late-instar larva (Mt. Ranier, Washington), maxilla, ventral aspect, showing fringed galea (*fga*).

ferences seem to represent loss or fusion of structures such as epicranial lines, a clypeal suture, ocelli, and distinct tergal plates in the Ptiliidae as well as the reduction of urogomphi from a two-segmented to a single-segmented condition. In all these features, and in others such as the frequent loss of spiracles, the Ptiliidae can be regarded as being in a derived condition with respect to the character states represented in the Hydraenidae, possibly resulting from evolution to a smaller size. The finger-like galea of *Ochthebius* and *Meropathus* in the Hydraenidae appears to be a derived condition since a typical Leptinid fringed galea is found in *Hydraena*. The two families, Ptiliidae and Hydraenidae, share an apparently unique character in the Staphylinodea—the pair of anal claws or hooks in the protrusible anal membrane of the Xth abdominal segment (lacking in *Meropathus*). These structures are probably used for purchase in locomotion. In one slide preparation of a *Pteryx* larva, there appeared to be a long slender muscle which seemed to be attached to the base of each claw and which apparently originated in the anteroventral part of segment VIII. Though no other Staphylinodea are reported to possess a pair of anal hooks, there are numerous fine crochets in this position in some Anisotomidae and Staphylinidae (e.g., Aleocharinae) at least. In the suborder Myxophaga, three pairs of anal spines are reported in *Sphaerius oven-sensis* (Oke) (Sphaeriidae) (Britton, 1966) and one pair of slender

processes in *Hydroscapha natans* Lec. (Hydroscaphidae) (Böving, 1914). Whether these structures bear any morphological relationship to the anal hooks of the Ptiliidae and Hydraenidae remains to be determined.

In summary, the Ptiliidae and Limulodidae are very closely related on the basis of larval characters, differing mainly in the loss of anal hooks in the Limulodidae. The two families also show numerous similarities to the Hydraenidae, Leptinidae, and Leiodidae, particularly in the possession (in most members of each family at least) of a unique structure—the fimbriate galea—which distinguishes the “Leptinid association” of Böving and Craighead (1931) from the remaining families of the Staphylinodea. Within the Leptinid association, the Ptiliidae share a unique feature—the pair of anal hooks—with the Hydraenidae, and clearly are closely related to that family on the basis of larval characters. The systematic affinities of the Hydraenidae, therefore, are with the Staphylinodea and not the Hydrophiloidea. Within the Staphylinodea, the Hydraenidae fall in the leptinid association on the basis of larval characters. However, it is evident that the detailed structure of characters such as the mandibles, maxillae, and anal hooks needs to be studied more thoroughly to determine homologies or convergence. It is also clear that our knowledge of the distribution of these characters and their states in the various taxa needs to be expanded before definitive phylogenies can be attempted.

The following modified key to the families is based largely on the revised key of Hinton (1941), but incorporates the new or revised data on the characters of the Ptiliidae and Limulodidae larvae of the present study.

KEY TO LATE-INSTAR LARVAE OF THE FAMILIES OF THE “LEPTINID ASSOCIATION” OF THE STAPHYLINOIDEA. (Modified from Böving and Craighead, 1931, and Hinton, 1941).

1. Mandibles with a large asperate or tuberculate molar portion¹ (Leptinid association). 2
 Mandibles without an expanded mola
 (other families of Staphylinodea—not included in key)
2. Anal membrane of abdominal segment X with 2 curved claws or hooks; larvae minute, usually less than 2.5 mm. long. 3

¹Molar area greatly reduced in the beaver parasite *Platypsyllus castoris* (Ritsema) (Leptinidae). In *Agathidium* (Leiodidae) the enlarged molar area is smooth and lacks a grinding surface (A. Newton, pers. comm.).

- Anal membrane without 2 prominent claws; with or without numerous fine crochets 5
3. Urogomphi 2-segmented; epicranial lines present; ocelli (4-5 on each side) present Hydraenidae¹
 Urogomphi 1-segmented or absent; epicranial lines absent; no ocelli (except in "*Nossidium*" from Panama which has a pigmented eye spot on each side) (Ptiliidae) 4
4. With 1-segmented urogomphi; galea fimbriate; most Ptiliidae
 Without urogomphi; no detectable fringed galea; larvae minute, long, cylindrical; habitat: spore tubes of fresh polypore fungi
 Ptiliidae, in part (*Nanosella*, *Throscophilum*, and allies)
5. No epicranial lines; ocelli or eyespots lacking; all body setae simple. 6
 Epicranial lines present; ocelli present or absent; compound setae often present
 Leiodidae (includes Catopidae, Anisotomidae)
6. Mandibles with slender articulated prostheca; urogomphi one-segmented
 Limulodidae
 Mandibles without a moveable, articulated prostheca, at most a fixed tooth-like projection; urogomphi 2-segmented. Leptinidae

ACKNOWLEDGEMENTS

I am indebted to Dr. Walter R. Suter, Carthage College, for many of the larvae described in this paper. Dr. John A. Wagner, Kendall College, some years ago located the stables which have been the source of the large *Nephanes titan* populations that have permitted firm associations of the larvae with the adults. Dr. Stewart B. Peck, Carleton University, Ottawa has provided larvae of *Pteryx* and, in the related family Leptinidae, of *Leptinus* sp. and the beaver lodge inhabitant *Leptinillus validus*. The *Ptomaphagus hirtus* larvae came from a laboratory culture being maintained and studied by Dr. Peck. Dr. John W. Lawrence, Museum of Comparative Zoology, Harvard University, collected the Panama *Nossidium* larvae, which were called to my attention and received through Dr. Alfred F. Newton of the same institution. Dr. Newton also provided specimens of *Hydraena* larvae (Hydraenidae). Dr. William L. Brown, Jr., Cornell University, identified the host ant of *Limulodes parki*. I am especially indebted to Drs. Peck, Lawrence, and Newton for instructive discussions and help about problems of Coleoptera larvae. Dr. Lee Herman, American Museum of Natural History, read the manu-

¹Anal hooks reportedly absent in *Meropathus* (Paulian, 1941).

script and contributed a number of suggestions that have been incorporated. Finally, the paper was critically read and reviewed for publication by Drs. Newton and Lawrence. I am indebted to these two colleagues for numerous suggestions and corrections, particularly as to terminology and nomenclature, exceptions and problems in using the key to families, as well as many other points.

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